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STATE OF NEW YORK

# Thirty-second Annual Report

of the

# New York State College of Agriculture at Cornell University

and of the

# Agricultural Experiment Station

Established under the Direction
of Cornell University
Ithaca, New York

1919

VOLUME I

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# THIRTY-SECOND ANNUAL REPORT

OF THE

# New York State College of Agriculture at Cornell University and of the Agricultural Experiment Station Established under the Direction of Cornell University

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STATE OF NEW YORK

DEPARTMENT OF AGRICULTURE

ALBANY, January 15, 1920

*To the Honorable the Legislature of the State of New York:*

In accordance with the provisions of the Statutes relating thereto, I have the honor to transmit herewith the Thirty-second Annual Report of the New York State College of Agriculture at Cornell University, as a part of the Twenty-seventh Annual Report of the Commissioner of Agriculture.

CHARLES S. WILSON,
*Commissioner of Agriculture.*

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# NEW YORK STATE COLLEGE OF AGRICULTURE

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Olin Whitney Smith, B.S., Assistant Registrar.
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# AGRICULTURAL EXPERIMENT STATION

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## PRESIDENT'S LETTER OF TRANSMITTAL

June 30, 1919

The Governor of the State of New York,
Albany, New York.

The Secretary of the Treasury,
Washington, D. C.

The Secretary of Agriculture,
Washington, D. C.

The Commissioner of Agriculture,
Albany, New York.

The Act of Congress, approved March 2, 1887, establishing Agricultural College Experiment Stations in connection with the Land Grant Colleges, contains the following provision: "It shall be the duty of each of said stations, annually, on or before the first day of February, to make to the Governor of the State or Territory in which it is located, a full and detailed report of its operations, including a statement of receipts and expenditures, a copy of which report shall be sent to each of said stations, to the said Commissioner of Agriculture, and to the Secretary of the Treasury of the United States."

And the Act of the Legislature of the State of New York, approved April 12, 1906, providing for the administration of the New York State College of Agriculture at Cornell University, contains the following provision: "The said University shall expend such moneys and use such property of the State in administering said College of Agriculture as above provided, and shall report to the Commissioner of Agriculture in each year on or before the first day of December, a detailed statement of such expenditures and of the general operations of the said College of Agriculture for the year ending the thirtieth day of September then next preceding." This was amended by the Act of April 3, 1916, which changed the fiscal year to end June 30.

In conformity with these mandates I have the honor to submit on behalf of Cornell University the report of the New York State College of Agriculture for the year 1918–19.

There are two sets of needs which the College has at the present time. The first is emancipation from a budgetary domination that cripples the

educational work of the College. The best interests of the College are not in contradiction with a budget, and an itemized budget, as the State wisely prescribes. But a more flexible budget is absolutely indispensable. The rigidity of the present budget entails serious losses to the College without any advantage to the State. An educational institution cannot in its financial administration be adjusted to the Procrustes bed which may be suitable for an entirely different class of institutions. If the state authorities will examine this matter carefully, they will, I am confident, give the College the relief it now asks for.

The other needs which the College now has cannot be satisfied without additional expenditures. I refer, first, to the higher compensation for the members of the teaching staff which changed economic conditions now render imperative. In the requisitions which the College has presented to the state authorities, salary advances have, however, been kept down to a minimum. And, besides these advances in salaries, the College is in need of new buildings, which its growth and the expansion and improvement of its work have now made absolutely necessary. These will be presented to the Governor and the Legislature at the earliest suitable moment. I bespeak for them the sympathetic consideration which their importance deserves.

Respectfully submitted,

JACOB GOULD SCHURMAN,

*President of Cornell University.*

# REPORT OF THE DEAN
# OF THE NEW YORK STATE COLLEGE OF AGRICULTURE

June 30, 1919

*To the President of the University:*

Sir: I have the honor to submit herewith a report of the work of the New York State College of Agriculture for the academic year 1918–19.

## The College of Agriculture and the so-called "budget" system of state appropriations

The question of most far-reaching importance before the State College of Agriculture at the present time is the effect of the form in which state appropriations are made on the maintenance and the vitality of the College.

In a democracy, education for all the people is fundamental. Progress comes through increased intelligence, through the acquirement and utilization of new facts and processes. The United States, during the Civil War more than a half-century ago, launched out on a nation-wide system of agricultural colleges, and later a similar system of experiment stations. With all their shortcomings, freely acknowledged, the land-grant institutions have been important factors in the promotion of agriculture and country life. They have become the state agricultural colleges and now receive most of their support from the state legislatures.

They have but comparatively recently reached a stage of large usefulness as educational and research agencies and attained an intimate and helpful relation with farmers. They had to find themselves and their work, and the discovery, though somewhat slow, has proceeded a considerable way.

At the time when these institutions have at last acquired large equipment and carefully trained faculties, when they have begun to render the aid to agriculture for which they were created, they are confronted with a system of state fiscal domination which is ruinous, and which if not stopped and turned about will reduce their efficiency immeasurably and remove from their faculties the kind of men and women on whom their life and vitality depend. This system is showing itself in various forms and in greater or less degree in several States. It has settled itself on New York State in almost perfect completion. I refer to the system of state appropriations for education and research in an itemized or segregated appropriation act whereby every salary of every employee is rigidly fixed by

legislative enactment and cannot be changed. The heads of these institutions are required to indicate, from eight to ten months before the beginning of the succeeding fiscal year, the exact minimum salaries required to maintain their faculties during that year and extending to a period approximately twenty-one months after the requests are filed. If it were the practice of legislatures to provide liberal salaries for teachers, this system would be less harmful, even though none the less unwise. But salaries are low, increases come slowly, and very seldom, if ever, is the legislature able to grant all of the needs expressed by the heads of the institutions. Adjustments in salary are imperative from time to time, to save necessary men.

With segregated appropriations the head of an institution loses the first essential to successful administration — the control of salaries. As an example: Some time ago this College had in a particular department a capable man to whom it was paying $1800. He received an attractive offer to go elsewhere, and, as the College could not increase his legislatively fixed salary, he left. A $1200 man was put in his place, and $600 on this salary was allowed to revert to the State. The College could as well have paid this new man $1800, for the salary was available; but his training and experience did not warrant it. Shortly afterwards two other competent teachers, each of whom was receiving $1200, received offers of $1800 and $1700, respectively, from other institutions. Both of them told the Dean that they would remain here at $1500. Their salaries were fixed by law at $1200, and the supposedly responsible head of the institution could do nothing, even though he was allowing the necessary amount of money to go back to the State from another salary. So both these men left also, and the institution lost three teachers experienced in the particular work of the College. These are single typical instances selected from among a very great number.

One of our outstanding teachers who is receiving $3000 has recently been offered $4500 in another position, but will remain here if he can be increased to $3500. A second highly trained man in the same department, who is receiving $2000, has been offered $3000 elsewhere but will remain if he can be given $2500. An assistant at $1150 has been offered $1600 by the Federal Government but will remain if $150 can be added to her salary. An extension professor at $3000, who has been under incessant demand by farmers in all parts of the State and who has waited many years for adequate recognition of his services by the State of New York, is just leaving to accept $5000 elsewhere. How long can this process continue and New York State have a College of Agriculture worthy of the State or able to render useful service to the agricultural industry?

This is typical of the situation constantly confronting us. The Legislature has adjourned. None of these increases are provided in the appropriation act passed by the recent Legislature, which fixes the salaries of these teachers for the twelve months following next July 1. Can these teachers be asked to wait a year, and in addition accept the hazard that promotions recommended to the next Legislature may not be granted? At the time this is being written, because of losses from the staff and the appointment of less competent persons to the positions, there are forty-three statutory positions on which less than the full amount available is being paid to the incumbent and the balance is reverting to the state treasury. We have a right under the law to give these persons the full amount available. Money could be found in the appropriations now available to retain the teachers mentioned above, no one of whom the College and the State can afford to lose. But the appropriation act says: "The salary or compensation of any officer or employee * * may be fixed by the * * officials appointing such officer or employing such employees at a less but not at a greater sum than the amount herein appropriated for the salary or compensation of such officer or employee." It provides further that "Any appropriations made by this act for salary, compensation or expenses shall be the salary, compensation, or expenses for one year of the officer, employee, * * * for whom the same is appropriated." What recourse is there to the authorities of an institution to hold men who they know cannot be allowed to go without imperiling the teaching standards or disrupting investigations long under way and into the prosecution of which much state money has already gone?

Is this economy? Is it efficiency? Is it good administration of the State's business? Will it build or maintain the kind of institution that will do credit to New York or any other State? Will it serve the people? Can any institution live under it and long retain vitality? One who has had experience with the segregated appropriation act applied to educational work can scarcely conceive of a system that would more certainly and effectively destroy these institutions.

The segregated appropriation makes the head of the College an automaton. He is charged with carrying out a specific detailed direction as to what personal service or equipment or printing shall be used for the work of his institution. He has lost administrative discretion. His chief work becomes at times — one has the feeling that it is most of the time — explaining to his staff why he is powerless to do what they want or to grant what both he and they know the work requires, and in endeavoring to persuade them to be content and to remain with vague assurances that things may be better a year or two hence. The institutions are largely administered by a printed appropriation act.

The persons placed at the head of our public institutions, who are presumably the best-informed representatives of the people in the administration of these particular institutions and who alone can know their changing needs, are not trusted in the use of appropriations for salaries. Is democracy to lose faith in the integrity of its members? Is it better for the State that these salaries should be itemized, fixed, and published broadcast so that all may know, than that the State's business should be responsive to the constant and inevitable adjustments and readjustments which go on incessantly in every efficient business? Do the people want the money well spent, or is it better that it be spent according to a printed price list? Is the great consideration human efficiency or mechanical efficiency? The segregated, minutely itemized budget is an expression of mechanical efficiency which lacks the breath of life. It reflects the accountant, not the administrator. It expresses the desire for accounting procedure and ignores the fundamentals of successful administration. There is grave danger, if not, indeed, actual certainty, that exactitude in accounting procedure and standardization of the State's business will menace the public welfare.

Economy is the claim. It is not economical. It will in time make the State the most inefficient employer of labor. The competent persons will be drawn off and the less competent left behind. This is now taking place. Such an institution as this seeks the kind of men that other institutions and enterprises want, men who by virtue of their ability are sought after. In this institution we have gathered our present staff from men who have been trained in from forty to fifty institutions throughout the country — wherever we could get the best for the money and opportunity available. Such men are not easily engaged nor easily replaced. Woe betide these institutions if they are gradually to become manned by the kind of persons that other institutions do not want — the men who are not picked out and therefore will stand without hitching beside a segregated appropriation act.

I have no criticism of the men in charge of financial matters in our own State Legislature. They are competent men, discharging their heavy responsibility with careful discernment. Their attitude toward the College and the Experiment Station has been considerate and sympathetic. And the development of this sort of state administration is not confined to New York. It is a tendency threatening the public educational institutions and experiment stations in many States. It is in the air.

I am in the fullest sympathy with the desire to establish methods which will assure honest expenditure of public funds and which will protect the State against either waste or misuse. I fully approve the most exacting accounting of expenditures of public funds. The public should know,

so far as it can know, that it is getting what it provides appropriations for. It is desirable that requests for appropriations should be filed with the Governor and the Legislature by the heads of the State's institutions in such detail as will enable these officers to act intelligently on the requests. Itemization in budget proposals is imperative if appropriations are to be intelligently made. But segregation in appropriation acts is absolutely deadening, especially in such an institution as this.

I am fully convinced that there is no question of larger importance confronting this College for the consideration of the President and Trustees of the University and the people of the State. Unless relief is forthcoming soon, I am persuaded that nothing can prevent the loss to the College of large numbers of its most valued teachers and investigators, who are now being retained only with the greatest difficulty. As able teachers cannot be held under the existing conditions, neither will strong teachers be attracted to take their places in an institution thus handicapped. The present situation is perilous. Responsibility falls heavily on those charged with the administration of the State College of Agriculture and the State's affairs to see that no stone is left unturned to accomplish a speedy release from the existing impossible system.

## The year in the College of Agriculture

The close of the academic year 1918–19 finds healthy progress being made in the State College of Agriculture toward recovery from the disturbances occasioned by the war. The outstanding condition that reveals the marks of the war is the absence of the great numbers of students which prior to the war taxed every facility of the College. In the fall term of the present year, when the war was at its height, there were registered in this College 654 students, of whom 259 were women and 301 were in the Student Army Training Corps. With the abrupt termination of the S. A. T. C. just before the end of the fall term, there were some losses among the students enrolled, but these were more than made good by former students who returned to the University. In the second term the registration of undergraduates reached 697. There were 100 graduate students taking work in the College of Agriculture, and 83 students in the winter courses, making a total of 880 students receiving instruction in agriculture. The registration for the spring term is identical with that for the preceding term, excluding the winter courses.

Agriculture not being a preferred subject for S. A. T. C. students (with the exception of biology and meteorology), the members of the staff of the College were variously employed during the fall term in what appeared to be the most useful ways: a number took leaves of absence without salary to engage in forms of war work; some taught sections required

of S. A. T. C. students in other departments; a larger number aided in meeting the increased demands in the extension work; still others utilized their time in overhauling laboratory equipment, revising lecture and laboratory outlines, assembling class material, developing herbaria, and preparing for publication valuable data that had been accumulated; many welcomed the opportunity to devote extra time to research in their chosen fields. The respite from continuous teaching was not unwelcome, therefore, and the time was advantageously employed in productive work.

Recognizing the desire of returning students to complete their requirements for graduation as quickly as possible, the faculty of the College of Agriculture waived the specific residence requirement of eight terms so as to permit students to graduate as soon as the scholastic requirements had been met. Every consideration consistent with the requirements of the work has been accorded to students who have been absent on war service.

## The teaching staff

The year has witnessed important changes in the teaching staff. On October 1, 1918, James E. Boyle, Extension Professor in Rural Economy, a specialist in problems of marketing and cooperation, entered upon his duties at the College. On the same date Dwight Sanderson came to the College as Professor and head of the Department of Rural Organization. His appointment marked the beginning of formal recognition of the important social problems of country life. On October 1, also, Homer C. Thompson, formerly of the United States Department of Agriculture, became Professor of Vegetable Gardening in the Department of Farm Crops, assuming the task of reorganizing the teaching and extension in vegetable gardening which had been seriously disturbed by loss of several teachers from the staff. On April 1, 1919, Warren S. Thompson, formerly of the University of Michigan, was appointed Acting Professor of Rural Organization.

On July 1, 1918, J. H. Voorhees came to the College as Assistant Extension Professor in Farm Crops, in which field the requests from farmers for aid had gone far beyond the capacity of our staff to meet them. On October 1, Miss Lula Graves was appointed Acting Assistant Professor in Home Economics to give instruction in dietetics in special courses arranged for the training of dietitians for war service.

On November 1, 1918, Professor E. L. Griffin, State Leader of Junior Extension, resigned to accept a position at the University of California, and was succeeded by Professor William J. Wright, for many years Director of the New York State School of Agriculture at Alfred University. On October 1, Assistant Extension Professor E. M. Tuttle, who for many

years had conducted the Cornell Rural School Leaflet, resigned to enter the army. On November 20, Assistant Professor C. T. Gregory left to accept a position in Plant Pathology with the United States Department of Agriculture in its cooperative work with Purdue University. On January 1, 1919, Assistant Extension Professor W. W. Warsaw resigned to enter commercial work.

Throughout the year Assistant Professor E. R. King has been absent in the army aviation service. On January 1, 1919, Professor S. N. Spring was granted leave of absence for the remainder of the year in order to engage in Y. M. C. A. work overseas, where he has been active in both hut and educational work. He will resume his post in the Department of Forestry on July 1. On January 1, Professor A. B. Recknagel, of the Department of Forestry, was granted leave of absence for the remainder of the year to continue his special work with the Empire State Forest Products Association. During the summer of 1918 he had been engaged on a timber census of New York State, undertaken at the request of the United States Government, with the purpose of gathering statistics of available lumber for use, especially for the navy. Professor A. C. Beal, of the Department of Floriculture, and Professor John Bentley, of the Department of Forestry, were on sabbatic leave of absence during the winter and spring terms.

On December 20, 1918, death claimed J. H. Bromley, Soil Surveyor in the Department of Soil Technology. He was a young man of excellent training and large promise, and his death caused a serious loss to the Department with which he had been associated.

## Prizes and scholarships

**The Eastman Prizes.** Through the generosity of A. R. Eastman, of Waterville, New York, there has been provided since 1910 an annual prize of $100 for speaking on questions of public interest to agriculture and country life. The contest for this prize, known as the Eastman Stage, has been open to both regular and special students of the College and has been held in the annual Farmers' Week. Mr. Eastman has recently given the University $3000 in 4-per-cent Liberty Bonds for endowing the stage permanently. The proceeds will be divided into prizes, the first of $100 and the second of $20. This prize has been eagerly contested for each year by large numbers of students, and to a very marked degree it has accomplished the purposes of the donor. It has given an impetus to public speaking in the College and to the preparation of original orations, which has been notable. Mr. Eastman's generous gift is a permanent benefit to the College and to its work for the State.

**Ring Memorial Prizes.** The interest on the Ring Memorial Fund, established by the bequest of Charles A. Ring, of Newfane, New York, becomes available for use after July 1, 1919. These funds are to be devoted to establishing the Ring Memorial Prizes, as follows: a first prize of approximately $30, and a second prize of approximately $20, to be awarded to undergraduate students in the College of Agriculture who, in essays reviewing the literature on problems in floriculture, vegetable gardening, and pomology, show the highest ability to evaluate scientific evidence. Rules governing the award of these prizes have been formulated by a committee from the departments of the College represented in the three fields of investigation. The donor of these prizes, long an esteemed friend of the institution, was especially devoted to the promotion of horticulture, and his gift has been applied to the furtherance of the work of his particular interest.

**Students Association Prize.** The Former Students Association of the College of Agriculture has established an undergraduate prize of $25 to be awarded annually at the close of the junior year to the student of good moral character who has maintained the best record and scholarship during his three years at the University. The award of this prize is made by the faculty of the College. The interest and support of its former students in promoting scholarship is an invaluable asset to any institution.

**Beatty Agricultural Scholarships.** The will of Harrison L. Beatty, late of Bainbridge, New York, provides a sum of $5000, the income from which is to be used for three equal scholarships in the winter course in agriculture or a similar course of study in agriculture, to be awarded through competitive examination to residents of Chenango County, one of them to be a resident of the town of Bainbridge. Regulations governing the award of these scholarships have been formulated by the Committee on Scholarships of the faculty of the College of Agriculture, and have been approved by the Board of Trustees of the University. These scholarships are known as the Beatty Agricultural Scholarships. This generous bequest will enable many young persons, who could not afford the expense without such aid, to obtain instruction at the College, and is a foundation that will yield constant returns in enriched lives.

## Changes in requirements for entrance and for graduation

The gradual introduction of agriculture into the curriculum, and the development of a four-years program in agriculture, in the high schools of the State, have necessitated a revision of the entrance requirements of the College. Students graduated from the high-school course and receiving the state vocational diploma in agriculture or in home making

do not meet the college requirements hitherto in force since they have received no instruction in foreign language. Some adjustment was imperative, since a break with our own natural constituency must result if students who have taken an interest in agriculture and home-making subjects in the high school are to be debarred from entrance to this College. The college faculty began formal consideration of this problem in the January meeting, and its recommendations were adopted by the university faculty. The requirements were changed so that students holding the New York State vocational diploma in agriculture or home making, or having had equivalent training, are admitted. To counteract the extreme specialization in agricultural science which would be possible, such students are required to elect in their college course an amount of work in foreign language, English, philosophy, political science, history, economics, political and social science, or mathematics, corresponding to their entrance shortage in foreign language under the old requirements.

The changes made in the requirements for graduation are less striking, and resulted largely from the demand for more flexibility than was afforded in the former curriculum in the choice of sciences leading to the various lines of specialized work in the College. The total amount of such work was not greatly changed. The one hundred and twenty hours required for graduation must now include forty-five hours in English and the fundamental sciences, fifty-five hours in technical agricultural subjects, and twenty hours to be elected either in this or in any other College in the University.

### The practice requirement in home economics

Corresponding to the requirement of farm experience on the part of the men, there has now been established by the faculty a requirement of home-economics practice on the part of the women. The requirement is equivalent to at least ten weeks of practice work and must be completed before the student enters her senior year. The requirement is needed to insure a better background of experience for the student's college work, and also as a basis for judging her capacity in relation to positions available for graduates. The establishment of the requirement will make it necessary for the College to help place these students in positions yielding the necessary experience, as is already done in the case of the men by the Office of Farm Practice.

### Free-tuition scholarships

Several years ago the Trustees established ten free-tuition scholarships to be awarded annually to worthy applicants from outside the State, and they have now added five to be awarded by the Dean to deserving

students from the devastated countries of Europe, preferably France, Italy, Belgium, Serbia, and Roumania. These scholarships are to carry free tuition for a period not to exceed four years, and the applicant must enter prior to the close of the academic year 1922–23. Efforts are being made to acquaint various agencies representing the countries named with the purpose of this action, and indications are that some if not all of these scholarships will be filled during 1919–20.

## Retirement of John Lemuel Stone

On February 15, 1919, John Lemuel Stone, Professor of Farm Practice, retired from the active work of his professorship under the statutes of the University. He entered the University in 1870 as a student in agriculture, and was graduated in 1874 with the degree of bachelor of agriculture, his class being the second in the University to contain agricultural students. He then returned to his home farm, where he became a leader in agricultural and civic affairs. Notable among his accomplishments during this period were his demonstration of the value of animal-feeding studies, the use of the ration, and the introduction of the silo. In 1897 he accepted a position at his Alma Mater on the invitation of Director Roberts. In 1903 he was given the title of Assistant Professor, and in 1907 was promoted to the professorship in Farm Practice. As teacher, extension worker, and manager of the college farms, he has served his University and the State with conspicuous success. Through his thorough knowledge of farm practice, coupled with a keen appreciation of scientific values, he was able to render large service to agricultural interests at a time when the colleges of agriculture were struggling for place and recognition. The farmers of the State will always be his debtors. As his colleagues in the university faculty said of him, "His inquiring mind, his practical sense, his ability in administration, his excellence as a teacher, and above all his lofty ideals, breadth of view, and capacity for friendship, have endeared him to his associates. He has richly earned the relief which retirement from active service brings."

As a mark of recognition, the Board of Trustees at its meeting on May 31, 1919, named the Agronomy Building, in which Professor Stone had worked for many years, Stone Hall.

## Changes in organization

At the meeting of the Agricultural College Council on April 12, 1919, on the recommendation of the Dean, two departments of instruction were discontinued as separate units. The Department of Drawing was dissolved, the free-hand drawing and the teachers concerned therewith being transferred to and merged with the Department of Landscape Art,

and the mechanical drawing and the assistant professor in charge being transferred to the Department of Rural Engineering. This change was a natural result of the growth and specialization of the latter two departments, to whose needs the Department of Drawing largely administered. The Department of Farm Practice was discontinued as a separate department of instruction, since it no longer has major teaching functions, and its staff and work were transferred to the central office of administration as an Office of Farm Practice and Farm Superintendence under the Dean.

At the same meeting of the Trustees, the Office of State Leaders of Home Demonstration Agents, heretofore attached to the Office of Administration of the Extension Service, was transferred to the Department of Home Economics and made an integral part of the extension work of that Department.

### Additions to equipment and facilities

Changes in the dairy industry in the State and the rapid expansion of the condensed-milk industry have laid on the College the necessity of offering regular instruction in milk condensing. The Department of Dairy Industry is now engaged in installing a small milk-condensing outfit for instructional purposes.

Through the Department of Rural Economy there was acquired for the University Library, in the past year, a set of the Howard, Bartels & Company reports on the Chicago markets from 1857 to date. A file of *Chicago Inter-Ocean* and its successor, the *Chicago Daily Tribune*, from 1880 to date was acquired by gift from the Chicago Board of Trade. The Department of Rural Economy also came into possession of the *Cincinnati Price Current* from 1846 to 1914. This paper was for many years owned and edited by the late C. B. Murray, and his daughter, Mrs. Corinne Murray Weddell (Mrs. Justin R. Weddell), of Cleveland, presented the valuable set as a memorial to her father. These gifts and purchases, supplementing valuable collections previously acquired, make Cornell University unique in such source material.

The College has recently purchased, with funds provided by the State Legislature, a tract of ten acres of excellent land in Monroe County for the development of field tests and demonstrations of selected farm crops, rotation schemes, and other agronomical work under soil and climatic conditions differing from those at Ithaca. Through the generosity of the President and Trustees of the State School of Agriculture at Alfred University, there has been made available to the College for an indeterminate period, presumably not less than twenty years, an area of ten acres on the school farm in the southern part of the State for similar purposes. For many years the College has rented an area at Virgil for

soil experiments. These arrangements mark the beginning of the acquirement of a number of field plots in the main soil and climatic areas of the State, for crop demonstration work. Other colleges of agriculture, both in the United States and in certain European countries, have made large use of such outlying fields in supplementing and confirming their experimental work at the central institution. These provisions constitute an important extension of our own work.

### The college library

An effort has been made during the year to catalog and classify all the books in the libraries in departments of the College, and the work is nearly completed. A beginning has also been made in adopting for the college library the method of cataloging used by the Library of Congress.

The college librarian has given special attention to what promises to prove a great reservoir to the library in the system of foreign exchanges. As soon after the armistice was signed as shipping conditions permitted, the College was enabled, through the Smithsonian Institution at Washington and without expense to itself, to send its bulletins and memoirs to more than five hundred foreign institutions with which it is hoped to establish regular exchanges. It is anticipated that this will bring to our library much material of great value to the College.

### The former-students conference

On June 20, 21, and 22, 1919, Cornell University celebrated its semicentennial in connection with the fiftieth Commencement of the University. It was an occasion long to be remembered in the life of the University — a great and stimulating home-coming of former students and teachers.

As part of the celebration, there was arranged a conference of former students and the faculty of each College, to consider the work and progress of the College, its present condition, its needs, tasks, and hopes for the future. For weeks in advance, committees had been at work on selected phases of the activities of the State College of Agriculture, and helpful reports were submitted to the conference for discussion. The subjects of reports and the committees preparing them were as follows: Administrative Organization and Policy, President A. Ross Hill, University of Missouri; Research and the Agricultural Experiment Station, Professor William C. Thro, New York Medical College of Cornell University, and E. H. Thompson, farmer, recently of the Office of Farm Management, United States Department of Agriculture; The Extension Service, Professor J. A. Foord, Massachusetts Agricultural College, G. C. Watson, farmer, Clyde, New York, and G. D. Brill, Manager Forsgate Farms,

Jamesburg, New Jersey; The Organization and Objectives in the Resident Teaching, Dean J. E. Russell, Teachers College, Columbia University, and R. J. Shepard, farmer, Batavia, New York. Many valuable suggestions for the future consideration of the faculty were contained in these reports. In addition, a committee from the faculty itself gathered many data from the faculty and from present and former students, which will furnish the basis of further studies by the staff.

In preparation for the celebration, and carrying out a purpose long in mind, the farms of the College were thoroughly posted with attractive permanent signs which acquaint the visitor with the nature of the experiment or the use of the field on every part of the farms. These guideposts are a valuable educational aid to students and to the large number of persons constantly visiting the experimental lands.

## The experimental work

The work of the Agricultural Experiment Station has continued throughout the year without abatement. Research is the function of the University that best differentiates it from other educational institutions. It is the part of the work that is most forward-looking. It is fundamental. Every encouragement that can be given to it, every provision to enable teachers so inclined to devote some time to original investigations, should be made. During the period covered by this report, special effort has been [illegible] to stimulate research in the College. There has been organized an informal monthly conference of the entire staff, to which graduate students also are invited, for the consideration of broad problems of research. These conferences have been addressed by Dr. W. H. Jordan, Director of the New York State Experiment Station at Geneva; Dean Eugene Davenport, Director of the Agricultural Experiment Station of the University of Illinois; Professor William Crocker, of the University of Chicago; Dr. L. H. Bailey, former Director of this station; Dr. H. P. Armsby, Director of the Institute of Animal Nutrition at Pennsylvania State College; and Dr. H. J. Webber, Director of Experiment Stations in California. This series of addresses by men eminent in agricultural research has been of great interest and profit to the staff and the graduate students.

There have also been organized during the year four group conferences on research, the groups being composed of members of closely related subject-matter departments, for the informal discussion of problems of immediate interest to the members of the group. It is hoped by this means both to accomplish better coordination in the research work of the College and to promote fellowship in the work.

The faculty of Agriculture has considered at length the advisibility of organizing a separate research staff, and has voted not to do so on the ground that the segregation of research workers would be opposed to the best interests of the College. There was the further consideration that in a university devoted to the stimulation of research and the advancement of knowledge, such a separation of workers was neither feasible nor desirable.

There is a growing tendency in the experimental work to establish friendly cooperative relationships with the experiment stations in other States and with the United States Department of Agriculture. As indicating the form which such cooperation may take, the following example will be of interest. The Department of Plant Breeding has long cooperated with the Office of Cereal Investigations of the United States Department of Agriculture. The study of corn genetics by our Department has now reached a stage at which it has been possible during the current year to arrange a more or less close coordination of effort on the part of this Department and men interested in the same line of work in the Experiment Stations of Wisconsin and Connecticut and in the Office of Crop Acclimatization of the Federal Department of Agriculture. Arrangements have also been made whereby some of the corn-color material, the genetics of which has been worked out here, will be studied chemically at the University of Michigan and physiologically at the University of Chicago. Certain of our corn materials have also been furnished for morphological studies at the University of Indiana. This is an example of the kind of cooperation that is likely to succeed. No attempt has been made to limit or direct any man's work, but by mutual agreement between men of our Department of Plant Breeding and men working in related fields elsewhere there has been effected a plan covering the field more adequately than would have been possible otherwise.

A detailed statement of progress in the work of the Experiment Station will be found in the departmental statements and the bulletins which form a part of this report. Some lines of work have been brought to conclusion; others have made progress; and new investigations have been undertaken.

### Investigation of bean production

The investigation of bean production, for which special appropriations have been made by the State, has been prosecuted with vigor, and the results thus far achieved give promise of bringing to the bean-growing industry substantial relief from the losses caused by insect and fungous enemies which have threatened to destroy the industry in the State. Summary reports of the three main lines of investigation follow:

## Report of the Plant Pathologist

(W. H. Burkholder)

The cause of the dry root-rot of the bean has been determined to be a fungus, which has been named *Fusarium martii phaseoli*. Its morphology and life history have been worked out and other hosts of the fungus have been found. The effect of weather conditions on the disease has been studied, as also the effect of the disease on the yield of the crop through several seasons. In controlling the disease, soil treatment has not proved to be beneficial. A strain of Marrow resistant to dry root-rot has been discovered.

The cause of the black root-rot has been proved to be the fungus *Thielavia basicola*. The distribution and general destructiveness of the disease, and the life history of the fungus, have been determined. Rhizoctonia causes a root rot of the bean, but this disease is relatively unimportant.

A White Marrow, a Red Marrow, and a White Kidney strain resistant to anthracnose have been developed through crosses with the Well's Red Kidney.

The numerous symptoms of bacterial blight have been determined and its systematic nature studied. Experiments have been conducted on varietal susceptibility and resistance to the disease.

Varietal susceptibility to bean mosaic, and the distribution and general destructiveness of this disease, have been determined. The Pea bean has been found to be the most susceptible variety. The Michigan Robust Pea bean is resistant to the disease.

## Report of the Specialist in Plant Breeding

(G. P. McRostie)

The 800 selections of standard field and garden beans from different parts of the country, with which the investigation started, have been reduced to less than fifty of the most promising from the standpoint of root-rot resistance and commercial usefulness. These remaining selections are being repeated this summer in different parts of the disease garden, to further sift out undesirable sorts.

This year we have more than 3000 plantings, over 2000 of which are second-, third-, and fourth-generation hybrids of crosses made with the object of getting good-yielding commercial types of beans resistant to three of the worst of the bean diseases in New York State — mosaic, dry root-rot, and anthracnose. We have now more than 100 white types resistant to anthracnose, a considerable number resistant to anthracnose and mosaic, and a number resistant to root rot and mosaic. The resist-

ance of these types is being thoroughly tested by repeated inoculations, and every effort is being made to separate desirable growth types as soon as possible.

More than 40 samples of the high-yielding, mosaic-resistant Robust Pea bean were distributed this year to growers in different parts of the State, in order to help introduce this type of bean as rapidly as possible into the Pea-bean districts of the State. The importation of this bean from the sections of Michigan where it could be obtained was also encouraged, and its purchase from the one source of supply in this State was advocated. In this connection it may be said that there are more than 200 acres of the Robust Pea bean planted in Orleans County this year. A few culling demonstrations are being given for the growers of the Robust Pea bean, in order to help them keep their seed as pure as possible.

## Report of the Entomologist

(I. M. Hawley)

The principal entomological investigations at the bean laboratory have been concerned with the seed-corn maggot (*Phorbia fusciceps*), the field gray slug (*Agriolimax agrestis*), and two flea beetles (*Systena frontalis* and *S. taeniata*). Notes have also been taken on many pests of lesser importance.

The study of the life history of the seed-corn maggot is nearly completed. Special study has been made of the conditions governing the emergence from hibernation and the egg-laying of the first generation of flies, with the idea of avoiding infestations of the maggots developing from these eggs. In 1919 beans were planted on May 15, and at intervals of about one week thereafter until June 30. It is planned to repeat this work in 1920. Seed beans have been treated with many substances tending to act as repellents. Some of these give promise of success. Studies of many fields where infestations have occurred have suggested preventives which will decrease the injury.

The field gray slug, a snail without the external shell, came to this country from Europe and causes immense loss to bean growers in wet seasons. In 1917 many beans were destroyed, but since that time more favorable weather conditions have prevented losses. The life history and habits of this pest are now well understood and many experiments have been tried to find a suitable control for the slugs. Of more than fifty materials tested in the field laboratory and the greenhouse, six give signs of control and will be tested in the field as soon as the opportunity occurs.

Two kinds of flea beetles are injuring bean fields in many places in the State. The study of the life histories and food plants of these species is

well under way, and field tests have developed a spray which gives almost complete control. In this work a special sprayer attachment has been developed for use on beans.

Other bean pests that have received attention are the bean cutworm, which eats the leaves and the pods; millipedes, which eat off the young plants; the wheat wireworm; the red spider; white grubs; leaf hoppers; and a leaf bug which has been shown to cause pitted beans by inserting its beak in the green pod.

Experiments in cooperation with Dr. Burkholder are now under way to learn what part insects play in the spread of the bacteria that cause bean blight.

### The game farm

The close of the first full year of operation of the game farm provided by the State for the experimental breeding and rearing of game finds the work well under way. Much time has been given to necessary improvements and repairs to buildings, and to equipping and stocking the farm. The number of pheasants reared was 525, of which 240 were turned over to the State Conservation Commission for distribution to the state game farms.

### The Extension Service

The work of reorganizing and strengthening the extension work of the College has been continued throughout the fiscal year 1918–19. Marked progress has been made in coordinating the work of extension specialists with that of the county agents, and in making the farm and home bureaus the agencies through which the major part of the extension work of the College clears.

On the resignation of the President of the University from the New York State Food Commission, the Director of Extension was appointed to fill the vacancy and he served as a member of that Commission until its recent dissolution. There has been close cooperation between the Extension Service of the College and some of the work of the Commission, particularly in conducting tractor schools and in making exhibits at fairs. The fairs in which the College took part by sending exhibits included the State Fair, the Rochester Industrial Exposition, the meeting of the New York State Horticultural Society at Rochester, the National Milk and Dairy Farm Exposition in New York City, and forty-six county fairs.

The twelfth annual Farmers' Week had a registered attendance of 3763, which is the largest attendance ever recorded at this College. The registered attendance is always considerably below the actual number of persons in attendance.

The extension work has been more widely developed and intensified in every department of the College during the year. The Offices of County Agricultural Agents and County Home Demonstration Agents, and the subject-matter extension specialists, have been under excessive pressure throughout the year to meet the multiplying demands from the county organizations. A detailed report of the extension activities will be found in the subjoined report of the Extension Service. It may suffice here to set forth in a brief statement the following outstanding features of the extension work during the current year:

1. The bending of the time, energies, and thought of the entire force toward the largest possible contribution to necessary and efficient food production and conservation, and, following the signing of the armistice, to assisting in the necessary readjustments of farming to a permanent basis.

2. The development and general acceptance of local organization on a community basis; and the making of community programs, especially by the county farm bureaus and to a less extent by the county home bureaus, in cooperation with the extension specialists of the College.

3. The organization of the work of the extension specialists of the College, in cooperation with the county agricultural and home demonstration agents, in the form of definite projects, and the consequent improvement in the correlation of the work of the extension specialists and the county agents.

4. The crystallization of the home demonstration work into permanent form, its extension to the cities, and its organization; with public recognition and acceptance and through permanent membership and local county appropriations, in twenty-five counties as a coordinate department with the agricultural extension work in the county farm and home bureaus.

5. A marked increase in the efficiency of the distribution and mailing of college publications, due to more detailed organization and supervision of the work.

6. The closer correlation of the farmers' institutes with other lines of extension work and programs, and a successful institute season under the first year of college management.

7. The largest use ever made of the Extension Service, in meetings and demonstrations, publications, and otherwise.

## *Publications*

The following publications of the College and Experiment Station have been issued during the year and distributed to the people of the State and to teachers and investigators in other States:

| | Number of pages in printed publication | Number of copies printed |
|---|---|---|
| MEMOIRS: | | |
| 13 Chlorophyll inheritance in maize (Department of Plant Breeding) | 68 | 3,000 |
| 14 The stimulation of root growth in cuttings by treatment with chemical compounds (Department of Botany) | 72 | 3,000 |
| 15 Insects injurious to the hop in New York, with special reference to the hop grub and the hop redbug (Department of Entomology) | 84 | 3,000 |
| 16 A fifth pair of factors, *Aa*, for aleurone color in maize, and its relation to the *Cc* and *Rr* pairs (Department of Plant Breeding) | 68 | 3,000 |
| 17 The translocation of calcium in a soil (Department of Soil Technology) | 32 | 3,000 |
| 18 A study of bacteria in ice cream during storage (Department of Dairy Industry) | 40 | 3,000 |
| 19 The effect of manganese compounds on soils and plants (Department of Soil Technology) | 40 | 2,000 |
| 20 The physiological action of nitrobenzene vapor on animals (Cornell University Medical College) | 68 | 2,000 |
| 21 Studies in the reversibility of the colloidal condition of soils (Department of Soil Technology) | 52 | 2,000 |
| 22 An analysis of the costs of growing potatoes (Department of Farm Management) | 104 | 5,000 |
| 23 The inheritance of the weak awn in certain Avena crosses and its relation to other characters of the oat grain (Department of Plant Breeding) | 48 | 3,000 |
| 24 A study of the plant lice injuring the foliage and fruit of the apple (Department of Entomology) | 88 | 2,000 |
| 25 The crane-flies of New York. Part I. Distribution and taxonomy of the adult flies (Department of Entomology) | 200 | 2,000 |
| 26 The dry root-rot of the bean (Department of Plant Pathology) | 40 | 3,000 |
| 27 The influence of low temperature on soil bacteria (Department of Soil Technology) | 40 | 3,000 |
| Total | 1,044 | 42,000 |
| EXPERIMENT STATION BULLETINS: | | |
| 398 Feed consumed in milk production (Department of Animal Husbandry) | 16 | 10,000 |
| 399 Experiments in fertilizing a crop rotation (Department of Soil Technology) | 16 | 5,000 |
| Total | 32 | 15,000 |
| READING-COURSE LESSONS FOR THE FARM: | | |
| 135 The farm ice supply (Department of Rural Engineering) | 24 | 40,000 |
| 136 The beef breeding herd in New York State (Department of Animal Husbandry) | 24 | 40,000 |
| 137 The dairy herd (Department of Animal Husbandry) | 24 | 10,000 |
| 138 Beginnings in beekeeping (Department of Entomology) | 24 | 40,000 |
| 139 Swine production in New York (Department of Animal Husbandry) | 36 | 10,000 |
| 140 The Babcock test, and testing problems (Department of Dairy Industry) | 32 | 10,000 |
| 141 Farm manure: its production, conservation, and use (Department of Soil Technology) | 32 | 10,000 |
| 142 Calculating the cost of milk production (Department of Farm Management) | 32 | 40,000 |

| | Number of pages in printed publication | Number of copies printed |
|---|---|---|
| READING-COURSE LESSONS FOR THE FARM (*continued*): | | |
| 143 Potato growing in New York (Department of Farm Crops) | 28 | 15,000 |
| 144 How the plant produces seed (Department of Botany) | 20 | 36,000 |
| 145 Planning the home vegetable garden: growing early plants (Department of Farm Crops) | 32 | 45,000 |
| 146 The problem of tuberculosis in cattle (College of Veterinary Medicine) | 28 | 50,000 |
| Total | 336 | 346,000 |
| READING-COURSE LESSONS FOR THE FARM HOME: | | |
| 120 Civic duties of women (Department of Home Economics) | 40 | 75,000 |
| 121 Sugar-saving desserts and confections (Department of Home Economics) | 8 | 200,000 |
| 122 How to use the apple crop (Department of Home Economics) | 12 | 200,000 |
| 123 A program of thrift for New York State (Department of Home Economics) | 8 | 50,000 |
| 124 Making a budget (Department of Home Economics) | 12 | 50,000 |
| 125 Self-study outlines for promoting thrift (Department of Home Economics) | 8 | 50,000 |
| 126 How to keep a cash account (Department of Home Economics) | 8 | 50,000 |
| 127 What to spend for food (Department of Home Economics) | 4 | 50,000 |
| 128 Points in selecting the daily food (Department of Home Economics) | 8 | 50,000 |
| 129 Questions for group discussions on thrift (Department of Home Economics) | 4 | 50,000 |
| 130 Club programs on thrift (Department of Home Economics) | 16 | 50,000 |
| Total | 128 | 875,000 |
| EXTENSION BULLETINS: | | |
| 30 Country milk stations: function, organization, operation, construction, and equipment (Department of Dairy Industry) | 32 | 5,000 |
| 31 The European corn borer (Department of Entomology) | 12 | 40,000 |
| 32 Soil survey of Yates County, New York (Department of Soil Technology) | 36 | 3,000 |
| 33 Making and storing butter for home use (Department of Dairy Industry) | 12 | 50,000 |
| Total | 92 | 98,000 |
| RURAL SCHOOL LEAFLETS: | | |
| September, 1918 (Department of Rural Education) | 264 | 40,000 |
| JUNIOR EXTENSION BULLETINS: | | |
| 1 First lessons in sewing (Department of Home Economics) | 44 | 10,000 |
| 2 Elementary garment making (Department of Home Economics) | 28 | 10,000 |
| 3 Rearing the dairy calf (Department of Rural Education) | 32 | 5,000 |
| 4 The vegetable garden (Department of Farm Crops) | 32 | 125,000 |
| Total | 136 | 150,000 |

| | Number of pages in printed publication | Number of copies printed |
|---|---|---|
| FARM BUREAU CIRCULARS: | | |
| 10 Annual report of the county agent leader for the year ending November 30, 1917 | 52 | 10,000 |
| MISCELLANEOUS: | | |
| Undergraduate course book | 40 | 500 |
| Plum spray schedule (Department of Entomology) | 2 | 5,000 |
| Total | 42 | 5,500 |
| ANNUAL REPORT FOR 1918 (in two volumes) | 1,472 | 2,000 |
| ANNOUNCEMENTS: | | |
| Announcement of courses, 1919-20 | 84 | 15,000 |
| Supplementary announcement of second, third, and summer terms, 1918-19 | 24 | 3,000 |
| Total | 108 | 18,000 |

SUMMARY

| | Total number | Total pages | Copies |
|---|---|---|---|
| Memoirs | 15 | 1,044 | 42,000 |
| Experiment station bulletins | 2 | 32 | 15,000 |
| Reading-course lessons for the farm | 12 | 336 | 346,000 |
| Reading-course lessons for the farm home | 11 | 128 | 875,000 |
| Extension bulletins | 4 | 92 | 98,000 |
| Rural school leaflets | 1 | 264 | 40,000 |
| Junior extension bulletins | 4 | 136 | 150,000 |
| Farm bureau circulars | 1 | 52 | 10,000 |
| Miscellaneous | 2 | 42 | 5,500 |
| Annual report | 1 | 1,472 | 2,000 |
| Announcements | 2 | 108 | 18,000 |
| | 55 | 3,706 | 1,601,500 |

## Detailed reports of departments

The following additional statements, made by heads of some of the departments, indicate the more important special activities and interests of those departments during the year.

### FARM MANAGEMENT

(G. F. Warren, Professor of Farm Management)

All of the research work begun in previous years by the Department of Farm Management has been continued, but owing to the various war activities it has not been possible to devote as much time to research as its importance justifies. Because of the importance of prices in adjusting farm activities, a constant study of comparative prices has been made.

War activities called for a very large amount of extension service and of work in connection with various food administrations. The state censuses for 1917 and 1918 were tabulated by this Department. The complete census report was published during the past year.

The Department has rendered a distinct service to milk consumers by showing costs of production and the probable effects of given prices on the future supply of milk. Without a knowledge of costs, it appeared to some persons that the price of milk was rising too rapidly. The cost data indicated that for two years the price of milk did not rise rapidly enough to maintain the dairy industry. The state censuses confirmed this by showing very material decreases in the number of heifer calves being raised. The cost data were used by the various milk commissions and resulted in the payment of more liberal prices than would otherwise have been allowed. They also tended to restore the confidence of the producers, and, while they did not prevent a decrease in the number of heifers raised, they prevented the decrease from being as large as it would have been. The importance of this is now clearly shown by the great shortage of dairy cows as a result of the failure to raise enough calves during the period when milk was relatively unprofitable. Had the price been much lower, what is now a milk shortage would have been much more serious.

During the year, 1135 farm records of a year's business were summarized. In this work a business analysis is made of the farm in order to determine ways in which it may be made more profitable. Since the farm demonstration work was started, 4770 such analyses have been made. In the past five years, 34,500 blanks for studying a year's business have been printed and used. These have been used by farmers, high-school teachers, and county agents, and by this Department.

During the year an improved form of farm inventory blank and a simplified farmer's cashbook were prepared. There were 5000 farmers' cashbooks sold, and 8000 inventory books. Previous to this year 5000 of the inventory blanks had been printed.

Instruction was given by members of this Department at 95 farmers' meetings and extension schools, with a total attendance of 6431.

## FARM CROPS

(E. G. Montgomery, Professor of Farm Crops)

The effect of the war on the experimental work of the Department of Farm Crops was to reduce it to projects which it was felt could not be discontinued without serious loss. This situation was due to the difficulty of obtaining labor. The most important piece of experimental work closed this year is the classification of American varieties of barley.

On July 1, 1918, the extension staff of the Department was increased to three men. Previous to this, Professor Barron had handled the work very largely alone. The most important piece of new work during the year has been the development of seed work which has to do with the standardizing of seed production. Among the larger features of this work may be mentioned the production of 24,000 bushels of seed corn on Long Island; the purchase of one carload of Grimm alfalfa for the State Grange, from the Northwest; getting information about seed sources which has proved very useful to the farm bureaus and to individuals. In addition to this, under the supervision of E. V. Hardenburg about 100,000 bushels of seed potatoes were inspected, 32,000 bushels were certified, and a large quantity were recommended for seed though not certified.

A better-seed train was run through western New York. The trip lasted 32 days and covered 17 counties. The average attendance to a stop was 37, and to a day was 69.

In vegetable gardening the principal work has been to develop home gardening. C. O. Smith has been added to the staff to look after the boys' and girls' project work in field and garden crops, in cooperation with the Department of Rural Education.

*Recommendations.* — As the Department is now about ready to develop its work in several lines, the need of a new building is felt. It will hardly pay to spend much on the building now occupied in order to develop the kind of laboratories and other special equipment needed by the Department. We shall be very much crowded when the normal number of students return. A new building will be very much needed in the course of two or three years.

The development of outlying experimental fields is a pressing need at present. Definite provisions should be made for this in the near future.

The main projects of the Department which should now receive development are: pasture improvement work; standardization and development of farm seeds; development of outlying experimental fields; crop surveys, including vegetable and canning crops; development of field work on muck crops.

Farm crops projects in 1919 were as follows:

| | Demonstrations |
|---|---|
| A way to grow alfalfa | 209 |
| Factors limiting success in alfalfa | 75 |
| Alfalfa varieties | 126 |
| Standardization and improvement of oats by breeding | |
| Class A | 8 |
| Class B | 20 |
| Local variety standardization | 35 |
| Spring wheat standardization | 14 |
| Bean varieties | 16 |
| Silage corn varieties | 387 |

| | Demonstrations |
|---|---|
| Silage corn — thickness of planting | 64 |
| Soybeans with corn | |
| Class A | 9 |
| Class B | 164 |
| Grain corn, Class A | 15 |
| Buckwheat | 1 |
| Sunflowers with corn | 12 |
| Potato standardization | 15 |
| Pasture improvement | |
| Washington County | 10 |
| Tioga County | 8 |
| Cayuga County | 1 |
| Rotation (lime, acid, clover, and so forth) | 200 |

### OFFICE OF FARM PRACTICE AND FARM SUPERINTENDENCE

(Asa C. King, Professor of Farm Practice)

War conditions broke up student schedules so completely that it was difficult to find time for any instruction in farm practice during the first and second terms of the year, when instruction had to be given almost entirely by arrangement with individual students. During the third term regular sections were held.

The rotation of crops on the college farm is being adjusted so as to bring into effect a five-years rotation on practically all of the fields within easy hauling distance of the barns. This rotation is corn, corn, oats, wheat, clover, and is determined chiefly by the large amount of silage needed by the Department of Animal Husbandry.

Land has been made available for the Department of Plant Pathology for experiments with wheat diseases and their control, and for work with potato diseases. Land has been provided also for the Department of Plant Breeding, to take the place temporarily of its plot, which was being drained.

The college farm has been run during the past three years without the purchase of any new equipment except what was absolutely necessary. In the spring of this year, however, a large amount of ditching was done. Fields 20 and 16, and the plant-breeding and floricultural fields, were partially drained, and a system of drains was started on the state game farm. Much of the equipment of the college farm now needs replacing. Other needs of the Office are the proposed coal pockets near the Blair barn, and a building for a farm boarding-house.

### PLANT BREEDING

(R. A. Emerson, Professor of Plant Breeding)

The extension work of the Department of Plant Breeding has been increased, and the teaching and investigation have been maintained, without serious interruption during the year, notwithstanding the tem-

porary loss of assistants owing to the war. This was made possible by the fact that practically all the members of the departmental staff remained in active service at the College throughout their vacation periods.

The Department naturally suffered a serious loss with respect to both graduate and undergraduate students as a result of the war. Graduate students are returning, and there is strong indication that normal pre-war conditions with respect to graduate study will be restored during the coming year. An encouraging feature of the situation with regard to graduate students is the considerable number of men holding positions of responsibility in other agricultural colleges who have made definite arrangements to come here on leave of absence for graduate study in plant breeding.

The investigations of the genetic principles underlying practical plant breeding have been continued about as in previous years. Numerous crop plants are employed in these studies. Papers presenting some of the results of this work, particularly with oats and corn, have appeared during the year as memoirs of the Experiment Station and as special articles in the standard genetic periodicals.

Some of the investigative work with small grains has been conducted, as in the past, in cooperation with other experiment stations and with the Office of Cereal Investigations of the United States Department of Agriculture. The study of corn genetics has now reached a stage at which it has been possible during the year to arrange a more or less close coordination of effort on the part of this Department and men interested in the same line of work in several other institutions.

The investigations of a more immediately economic aspect have had to do, as in the past, with the production of improved strains of staple crops. During the year this type of work has been undertaken with cabbage and rye, and work with oats, wheat, barley, corn, and beans has been continued. Two improved strains of oats and one of wheat have been tested in several sections and are now being grown in a fairly large acreage in certain parts of the State, replacing farmers' common stocks. These strains have been developed wholly through selection from the stocks commonly grown in the State. During the past year, certain strains developed through the hybridization of different varieties have given promise of outyielding even the select strains previously distributed.

Special bean investigations have been carried on at Perry during the summer and at Ithaca during the winter, in cooperation with the Departments of Plant Pathology and Entomology. The use of greenhouse space during the winter has made it possible to grow three generations of cross-bred plants in the year, while only one generation could have been grown had it been necessary to confine the work to the ordinary growing season. By this means, notwithstanding the fact that breeding

work necessarily requires the growing of many generations of plants, it has been possible, in the two years during which the work has been under way, to make very important progress in the production of strains resistant to the bean diseases that have been seriously injuring the bean industry of western New York. Already several desirable white beans have been produced that are resistant to the two forms of anthracnose, a few that are resistant to root-rot, and some that are resistant to mosaic; and a very promising beginning has been made toward combining into one strain resistance to all these most serious diseases.

The extension activities of the Department have been increased during the past year, notwithstanding the fact that the Department has had the services of only one extension man on half time. Three or four other members of the staff have helped with this work at times.

The principal increase in extension work has been concerned with oat- and potato-breeding demonstrations. In all its extension work, it has been the policy of the Department to conduct thorough-going work with a few farmers who are interested in growing and disseminating improved stocks, rather than to attempt to cover the entire State with plant-breeding propaganda. During the past year, help has been given to farmers in eight counties in making selections from which potato-seed breeding plots will be established. Demonstrations of the merits of two of our improved strains of oats, and of a stock grown by a Jefferson County oat improvers' association with which the Department has been cooperating, have been made in several counties. The planting, harvesting, and threshing of all these lots have been superintended personally by one or more members of the staff of this Department. The threshing has been done with a small threshing machine taken from place to place on a truck.

Help has been given to several farmers and to one seed-growers' association in the proper methods of selecting seed corn for increased yield and earliness. Demonstrations of the value of a new strain of Pea bean, which has been under test by the Department for some five years and which the Department of Plant Pathology has found to be immune to the mosaic disease, have been made in several bean-growing counties through the bean laboratory at Perry.

## BOTANY

### (K. M. Wiegand, Professor of Botany)

All members of the teaching staff of the Department of Botany, as well as all major graduate students, are engaged in some research. Thirteen titles are reported from the Laboratory of Plant Physiology, and seventeen titles from other laboratories of the Department.

The extension work of the Department has been confined to the following lines of work, in addition to lectures and demonstrations during Farmers' Week: (1) Correspondence with farmers and others in regard to weed identification, weed eradication, legume inoculation, and other matters. There were 250 letters sent out relating to weeds, and 2500 relating to inoculation. (2) Distribution of cultures containing the organisms for inoculating soil in preparation for legume crops. The number of these sent out was 8500. There were also 100 letters written relating to the culture of mushrooms.

The work of increasing the collection of illustrative material and herbarium specimens has been carried forward as in previous years. Many members of the Department have given a considerable part of their time to building up the illustrative material for the various courses in the Department. The number of sheets added to the herbarium during the year is about three thousand. The apparatus necessary for teaching and investigation has also been materially increased.

## PLANT PATHOLOGY

(H. H. Whetzel, Professor of Plant Pathology)

*Teaching.*— The total number of undergraduate registrations in the Department of Plant Pathology from July 1, 1918, to June 30, 1919, was 94, and the total number of graduate students doing work in the Department during the same period was 20. As a result of the marked reduction in the number of students to be taught during the early part of the year, many of the members of the teaching staff were turned to extension and research work.

*Research.*— Curtailment of the research work was made necessary by the demands for emergency and extension work during the period of the war. In general, however, the research work has not suffered as much loss as the teaching in this respect. Many of the important lines of research which were under way have been continued, and at least one new line has been taken up, namely, an investigation of the leaf-roll and mosaic diseases of potatoes. This study is designed to throw light as soon as possible on some of the urgent problems of disease in seed potatoes, at present the chief problem before the growers in this State. The objects of the investigation are to determine to what extent these diseases are responsible for the reduction in crop yields and to what extent they are transmitted from diseased to healthy stock, and especially to determine the relation of temperature and humidity and of soil factors to the development of these diseases. It is hoped also that effective measures can be worked out for the elimination of these diseases, especially from potatoes grown in the northern part of the State and used for seed on Long Island.

The work on bean diseases has been continued without interruption along the lines indicated in the report for last year. The progress on this problem is necessarily slow since it involves the development of resistant varieties by breeding and hybridization.

The work on diseases of cereals and other grasses has continued through a cooperative arrangement with the Office of Cereal Investigations of the United States Department of Agriculture. Extensive experimental plots for the study of cereal seed disinfection have been laid out and planted on the university farm.

Mycological investigations have been continued along two lines: first, taxonomic studies on the genus Botrytis, with an investigation of some of the diseases caused by species of this genus, particularly the diseases of tulips; secondly, taxonomic studies on the family Coryneliaceae. The latter work is practically completed.

*Extension.*— The extension activities of the Department have been directed chiefly along the following lines: (1) giving information to the farmer regarding his immediate problems; (2) teaching fundamental principles by means of extension schools; (3) making surveys for the procuring of more complete data concerning the distribution of the various more destructive diseases; (4) field demonstrations and inspections conducted by field assistants and extension specialists.

In the giving of direct information, nearly 125,000 leaflets describing the cause and control of diseases were distributed through the county agents, nearly 3000 personal letters were written, and six exhibits at state and county fairs were held.

One of the most important phases of the extension teaching was the seven demonstration schools held during the winter season. The total attendance was 1328, and 56 lectures were given. Aside from the schools, four institutes and thirty-three community schools were conducted.

A very careful survey was made of nearly all the common diseases injuring crops, but particularly the diseases of cereals.

The most effective work was accomplished by the eight field assistants who carried on disease work, in separate counties under the auspices of the county agents. Inspections were made of the fields and orchards, and advice based on the facts obtained from these inspections was given to the growers. In two of the fruit counties a special method for relaying spraying information was worked out and conducted by means of the telephone. Cooperative demonstrations of the relative values of commercial preparations as compared with lime-sulfur were given.

Demonstrations showing that onion smut could readily be controlled, saved for the muck growers a large proportion of their crop.

Inspections were made of many potato fields, and those showing the greatest number of plants free from disease were listed so that farmers were enabled to buy cleaner seed. Diseased and healthy hills were staked, and later the yields were weighed, showing concretely the losses due to diseases.

In all the extension work, not including exhibits, 7153 persons were given instruction in 55 counties of the State.

*Needs of the Department.*— The first and greatest need of the Department, which has been pointed out in every report for the past ten years, is proper housing. The situation is becoming intolerable. Not only are the laboratories and offices entirely too small for the work, but they are becoming increasingly filled with materials and apparatus, until there is practically no room for additions. Besides this, the actual number of offices and laboratories is wholly inadequate. There are not enough offices now to provide for the present staff with any degree of comfort. There is no lecture room and no recitation room. The *esprit de corps* of the staff cannot be maintained under these conditions. It seems that the Department should now receive consideration in the matter of better housing.

With regard to personnel, the Department is seriously handicapped in every division of its work, particularly in research and extension. In research there is need of a man to work on the diseases of fruit crops. During the period of the war no work along this line was under way. Fruit growing is one of the most important agricultural industries of the State, and the Department should have at least one man devoting all of his time to the diseases of fruit. Similarly, a man is needed for research work on the diseases of field and truck crops. Both these needs should be provided for next year if the College is to meet its obligations in this line of crop work in the State. There are other lines of research calling for consideration, and it is hoped that there may be a steady development of this work in the Department.

With respect to extension work, the transfer of Dr. Blodgett from extension to research leaves the Department greatly in need of some one to oversee the work of the special field assistants. Dr. Chupp gave up his vacation this year in order to assist in overseeing the work of these assistants, but neither he nor any one else should be expected to do this regularly. The extension staff of the Department should include a man whose duty it would be to oversee the extension work on fruit crops and another for the same work on field and truck crops.

So far as the teaching work is concerned, it is anticipated that additions to the staff, at least for some years, will not be above the grade of instructor. However, it will be necessary to have additional instructors and assistants

for carrying the work in the different courses if the Department is to meet the demands of an increased number of students within the next year or two.

## SOIL TECHNOLOGY

T. L. Lyon, Professor of Soil Technology

The members of the Department of Soil Technology who during the year were relieved of part of their teaching, owing to small enrollment, took the opportunity to engage in research. As in past years, the research work of the Department was conducted partly on the Adams Fund and partly on other funds. The Adams Fund project is "a study of the availability and utilization of plant nutrients in soils under different methods of treatment." The use of the lysimeters has been continued, and the first ten-years period of crop production will be completed at the end of the present calendar year, although the drainage water will not all have been collected until May 1, 1920. The soils will be resampled at that time. The part of the experiment dealing with the influence of the growing plant on bacterial processes in the soil has received much consideration during the year.

An experiment has recently been started to ascertain whether the injurious effect which grass often exerts on apple trees is one manifestation of the influence of the growing plant on bacterial processes in the soil. It seems possible that the injury may be due to a lack of available nitrogen, the supply of which has been curtailed by inhibition of the nitrate-forming process, for which the grass may be responsible. In this experiment the Department has the cooperation of the Department of Pomology at this station.

The experiment concerning the nitrogen balance in soil on which alfalfa and timothy have grown for a number of years, has been transferred to a number of small plots, surrounded by partitions, in all of which the soil was thoroughly mixed and sampled at the beginning of the experiment. It is expected that the work can be so controlled that the results will be more reliable than if the study were made with ordinary field plots.

*Soil surveys.*— In the season of 1918, the soil survey work covered two areas: Chenango County, which has an area of 894 square miles; and the White Plains area, embracing the counties of Westchester, Putnam, and Rockland, with an aggregate area of 864 square miles. The latter area includes much of the mountainous land in the southeastern part of the State, together with the agricultural land in the main suburban district. At the opening of the season of 1919, field work was begun in Wayne County. Most of this county was surveyed in 1902, when survey methods were very new, and it is desirable that it be resurveyed.

*Extension.*— The main lines of extension work in progress in 1917-18 have been continued in substantially the same form during the year 1918–19. All work in soils is grouped under Smith-Lever Extension Project No. 11. The activities may be tabulated as follows:

| | Number | Counties |
|---|---|---|
| Demonstration plots for which reports were received at the close of the field season of 1918 | | |
| Lime | 98 | 12 |
| Fertilizers | 36 | 11 |
| Lime and fertilizers | 4 | 3 |
| Manure | 1 | 1 |
| Drainage — Farmers assisted | 170 | |
| (Ditch opened by state ditching machines under surveys of this Department working in cooperation with the Department of Rural Engineering. To December 1, 1918) | 35,000 rods | |
| Number of days spent in field | 190 | |
| Number of farms visited | 153 | |
| Number of extension schools attended | 4 | |
| Half-days instruction given | 29 | |
| Number of persons attending | 155 | |
| Special conferences | 42 | |
| Attendance | 123 | |
| Lectures | 57 | |
| Attendance | 4,261 | |
| (These lectures outside of Farmers' Week) | | |
| Letters — Personal | 3,171 | |
| Circular | 40 | (circulation 2,339) |
| Articles written | 32 | |
| Number of pages | 186 | |
| Soil samples examined | 148 | |
| Soil acidity outfits distributed | 21 | |

*Publications.*— Publications of the Department aside from those issued by the University, which are listed elsewhere, are as follows:

Influence of higher plants on bacterial activities in soils. By T. Lyttleton Lyon. Journ. Amer. Soc. Agron., vol. 10, p. 313-322.

The county farm bureau and a national federation of agriculture. By Elmer O. Fippin. The Ohio Farmer, February 22, 1919, p. 320-321.

American potash in crop production. By E. O. Fippin. Cornell Countryman, April, 1919, p. 121-122, 140, 142, 144.

*Recommendations.*— For many years the College has analyzed samples of soils from different parts of the State. In spite of this, we have no systematic knowledge of the composition of these soils, because the samples were taken by persons who did not understand soil sampling

and the importance of recording the exact location, and so the sample could not be referred to the series and the type to which it belonged. If the samples were properly taken, the analyses would gradually provide the College with a body of knowledge of the soils of the surveyed areas of the State which would be of much value to our extension specialists.

While some progess has been made in providing for the experiment fields to be located in the important agricultural regions of the State, the last Legislature did not make a sufficiently large appropriation to permit the beginning of work on even one field. Efforts should be continued to get enough money to provide for the equipment and operation of at least two fields.

The building in which the Department is located is crowded to an extent that hampers scientific work. For the conduct of research in soils, space is needed for the drying and preparation of soils and plants for analysis and for many other operations. Such space was provided in the plans for the building, but owing to the assignment of it to other departments a point has been reached where the work in soils must be curtailed.

A frame structure with wire-netting sides and concrete floor is needed at the experiment field, for storing crops from the experiment plots before they are threshed. This structure should have a projecting roof to cover the concrete threshing floor, which is now unprotected from the weather. Such a building would cost not less than $2500.

While some of the plots on the experiment field have been tile-drained, there are still some that need drainage. Adequate drainage for all the plots should be provided as soon as possible. This has not been possible in the past because an outlet for drains on these plots could be supplied only through land occupied by the Department of Plant Breeding, and that land was not drained. Provision has now been made for draining that land, and therefore it will be possible to drain the remainder of our plots.

## POMOLOGY

### (W. H. Chandler, Professor of Pomology)

During the year covered by this report, Professor A. H. Hendrickson, of the College of Agriculture of the University of California, taught in the Department of Pomology at this College in exchange with Assistant Professor E. L. Overholser. Assistant Professor Overholser has now resigned his position here and will remain with the University of California.

The experiments in pruning old and young trees, hardiness studies, fertilizers for strawberries and bush fruits, osmotic relationship and incipient drying of fruit, and factors that influence the setting of fruit, have been continued. The work with color in fruits will probably be

discontinued inasmuch as Professor Overholser will take up this work in California. In addition to the above, a considerable study has been made of the resistance to water movement in trees and its relation to such practices as pruning. Under the hardiness studies observations are being made of the recovery of trees that were badly injured during the winter of 1917–18. During the year a large amount of data has been gathered as to the effect of that winter on the various fruit species and varieties.

*Extension.*— The extension specialists of the Department have participated in the following activities during the past year:

Extension Activities of the Department of Pomology

| Organization | Demonstrations | | Lectures | | Conferences | | Number of farm visits |
|---|---|---|---|---|---|---|---|
| | Number | Attendance | Number | Attendance | Number | Attendance | |
| Farm bureaus | 91 | 1,770 | ..... | ..... | 170 | 343 | 69 |
| Farm bureau community meetings | ..... | ..... | 11 | 474 | ..... | ..... | ..... |
| Demonstration schools. | 5 | 134 | 46 | 1,324 | 101 | 101 | 13 |
| Farmers' Week | ..... | ..... | 18 | 1,047 | ..... | ..... | ..... |
| Farmers' institute | ..... | ..... | 8 | 216 | ..... | ..... | ..... |
| Miscellaneous | ..... | ..... | 17 | 3,226 | ..... | ..... | ..... |
| Days in field — 249 | | | | | | | |

The Department is working in cooperation with the Niagara and Wayne County Farm Bureaus in establishing central packing-houses. It is also cooperating with the Greene County Farm Bureau in demonstrating the value of commercial fertilizers for apple trees in a rather infertile soil.

Because of special studies that have been made at this College concerning the effect of low temperature on fruit trees and concerning pruning, there was a considerable demand among fruit-growers' organizations in this State and elsewhere for the services of men in this Department. During the war addresses to eight such organizations outside the State were made and approximately 900 growers were addressed. The same subjects were discussed with practically all the local, in addition to the general, fruit-growers' organizations in the State, at their request.

A study has been made of the results apparently being secured from the reading course. It is the view of the extension workers in the Department that so few persons are reached who will actually use the information thus offered, that the benefits do not justify the loss of the time given by the workers in preparing these lessons.

*Recommendations.*— The important needs of the Department have been reported heretofore. For teaching purposes there is only one laboratory, 30x30 feet in size. This is entirely inadequate. The Department

should have in addition to this room, which is needed for graduate work, a large laboratory 30x40 feet in size for its large classes, a laboratory 30x30 feet for systematic pomology, and a stock room, or storeroom, 20x20 feet in size.

The Department has very serious need for cold-storage equipment and for an addition to the packing shed, in order (1) that the fruit grown experimentally and for teaching purposes may be handled and sold, (2) that certain experiments concerning the effect of low temperatures on plants may be conducted, and (3) particularly that we may have fruit and plants available for teaching and experimental purposes throughout the winter. An outstanding need for this is the preservation of fruit to be used in testing grading machinery for the cooperative packing organizations that are being promoted in the State.

The Department is also greatly in need of greenhouse space, both for teaching and for experimental purposes.

## FLORICULTURE

### E. A. White, Professor of Floriculture

The work at the experimental gardens of the Department of Floriculture at Craig Field has been carried on much as in former years. It is to be regretted that these gardens are so inaccessible to the public. The peony and rose test gardens, which are attractive and interesting places especially in June and July when the plants are in bloom, remain undiscovered by many even in the University and vicinity. An effort has been made to find a more central location, but suitable land seems unobtainable. The Department needs a tract of land, centrally located where it can be readily reached by classes and on which may be built a range of greenhouses for work along investigational lines in floriculture. If, however, the gardens are to remain on the present area, it is very important that an improved road be built to them from Dryden Road near the East Ithaca Station, or that Tower Road be widened and improved so that the gardens may be reached in rainy weather. It is now practically impossible to reach them after a rain.

The repairs on the barn have greatly improved the appearance of the garden area. During the year a considerable amount of tile drain has been laid, which has greatly benefited the soil conditions especially in the rose garden. The moving of the bungalow to a site in the rose garden has made possible a workable field office and a rest room for the many visitors who come to the gardens.

Cooperative work with the American Rose Society, the American Gladiolus Society, the American Sweet Pea Society, and the American Peony Society, is still being carried on as fully as the funds of the Depart-

ment permit. The organizations named do not finance any of the gardens, but assist in the work through their influence in obtaining from nurserymen, without charge to the College, plants and other material for investigation and research.

The Department of Floriculture is one of the few departments in the College in which no one is employed for extension work. The florists have problems which they want solved, and they would welcome assistance from the College. A man should be engaged who could keep in touch with the florists and who would be available also for giving the lectures on floricultural subjects which are called for from time to time. For this work a man should be selected who has had wide experience of a practical nature. He should have had also a thorough training in plant pathology and entomology, so that he could assist in solving the insect and disease problems with which the florists have to contend.

## FORESTRY

### Ralph S. Hosmer, Professor of Forestry

*Teaching.*— Almost every man enrolled as a professional student in the Department of Forestry entered some form of military service during the war. The two or three exceptions were students who either were under age or were disqualified because of some physical defect. The regular program of instruction was therefore necessarily much interrupted. In the summer term, because of the fact that the students in attendance were called to the colors, instruction was discontinued on August 24. In the fall term one course, Forestry 8, was rearranged to meet the needs of S. A. T. C. students, for whom it was especially offered.

Although of little value in themselves, yet, because of the unusual conditions which they reflect, the figures of attendance for the past year are given in the following table, in comparison with normal years preceding the war:

| Year | Registration in courses intended primarily for students from other departments | Registration in courses intended for both professional students and students from other departments | Registration in professional forestry courses | Registration in graduate courses | Total number of students registered in regular courses | Winter course | Summer school | Grand total |
|---|---|---|---|---|---|---|---|---|
| 1912–13.. | 213 | 56 | 143 | ..... | 412 | 47 | 22 | 481 |
| 1913–14.. | 139 | 80 | 131 | 40 | 390 | 57 | 28 | 475 |
| 1914–15.. | 115 | 107 | 214 | 52 | 488 | 20 | 18 | 526 |
| 1915–16.. | 300 | 196 | 189 | 33 | 718 | 17 | *..... | 735 |
| 1916–17.. | 279 | 186 | 215 | 32 | 712 | 36 | *..... | 748 |
| 1917–18.. | 99 | 69 | 61 | 8 | 237 | 10 | *..... | 247 |
| 1918–19.. | 140 | 78 | 62 | 0 | 280 | 6 | †3 | 289 |

* In place of regular courses during the Summer Sessions in these years, there was given a series of public lectures on forestry.

† Summer Session of 1918.

*Research.*— During the summer and autumn of 1918, Assistant Professor B. A. Chandler was engaged in an investigation of the results of cuttings made fifteen years ago at Nehasane Park, in the Adirondacks, under the direction of Colonel H. S. Graves (now Chief of the United States Forest Service). The original cuttings were made with the object of promoting the reproduction and increased growth of spruce. Professor Chandler's study was made under the general plan of forest investigation for the State prepared by the New York Section of the Society of American Foresters. The results of Professor Chandler's studies in the field were given in a paper read before the Section at a meeting held in Albany on January 22, 1919, and published in the *Journal of Forestry* for April, 1919. Under the same general program, permanent sample plots were laid out early in the summer, in a forest near Newcomb, New York, in cooperation with Finch, Pruyn & Company, Inc.

*Extension.*— The extension work of the Department in the past year may well be divided into two parts — that which was carried on before the signing of the armistice, and that which has developed since. Before the closing of military activities, much work was under way, and more was planned, to aid in fuel conservation by encouraging the use of wood fuel. This work was conducted in cooperation with, and as a part of the campaign of, the New York State Advisory Committee on Wood Fuel. A circular letter was sent to 1000 farmers in Tompkins County in an effort to locate fuel wood. The office of the Department of Forestry served as a clearing house between the producer and the consumer of wood. Efforts were started to encourage similar work in other counties. With the signing of the armistice this line of activity ceased.

Since January the extension work has followed more closely the lines previously laid out, with the view of assisting woodlot owners to know their holdings and to apply profitable systems of management to them. Marketing of woodlot products is becoming more and more a factor in this program. During the winter an effort was made to encourage the manufacture of maple sugar and sirup. The best results were secured in Cortland County, where the organization of a producers' cooperative association resulted in materially increasing the returns to the makers of maple products.

During the spring every opportunity was taken to encourage forest planting. Two demonstrations were held, in each of which more than 10,000 trees were planted. The New York State Conservation Commission reported that as a result of order blanks sent from this office, nearly 100,000 trees were shipped from the state nurseries to private planters.

Seventy-six days were spent in the field by members of the forestry extension staff, working in twenty-four counties. Nineteen demonstra-

tions were held, attended by 1972 persons. Sixteen lectures on forestry were given, attended by 1224 persons. Thirty woodlot inspections were made, including not only inspections of demonstrations and woodlots previously given attention by representatives of the College, but also the inspection of areas new to the Department on which work is contemplated. It is a common thing for demonstrations to develop as a result of these inspections. Twenty conferences and conventions were attended, at which the extension specialists met with 145 persons. Fifteen articles on forestry subjects were prepared, comprising a total of 29 pages. These were distributed partly through the college news service but also by agricultural papers.

*Publications.*— Cont ibutions from various members of the departmental staff have appeared during the year in the *Journal of Forestry*, in lumber trade journals, and in *New York Forestry*, the magazine of the New York State Forestry Association. Another volume of the forestry series published by John Wiley & Sons, New York, has been announced for June, namely, *Forest Management*, by Professors A. B. Recknagel and John Bentley, jr.

*Cooperation with other agencies.*— During the summer of 1918 Professor Hosmer held a temporary appointment as forester under the New York State Conservation Commission, in charge of a forest survey in the Adirondacks on a tract which may be acquired by the State as an addition to the forest preserve.

*Recommendations.*— The need that presses with most force on the Department at this time is for an increase in the salaries of members of the staff that will enable them to meet current everyday expenses with some degree of equanimity. Considering the present purchasing power of the dollar, it is impossible without outside income for professors to maintain their families even on the modest scale demanded in a university community. This results directly in two things that are to the detriment of the College: lessened efficiency of the staff, due to worry over financial problems; and the imminent danger that these men will, for that reason, be compelled to seek other positions. Unless the situation is speedily remedied, resignations of valued members of the staff are bound to follow.

The other needs of the Department can wait on the solution of the salary question, but it should not be forgotten that they remain for later consideration. One need which stands out at this time is for the firm establishment of research work in forestry — first, through adequate provision for at least two men of the investigative type, one in silviculture and the other in utilization; secondly, through proper equipment for the use of these research workers, especially in the way of instruments of precision for making the necessary records; and thirdly, as has been pointed

out in many earlier reports, through the acquisition of a college forest within easy reach of Ithaca, of some 2000 acres in extent, to be used for both investigation and demonstration.

Because it affects its teaching work, the Department is interested in the general building program of the College, and especially in the erection of a plant industry building. With the normal enrollment of students expected in the autumn of 1919 and in subsequent years, the curtailment in the number of lecture rooms and laboratories that has resulted from the unavoidable housing of a third department in the Forestry Building will be seriously felt. It is hoped that provision may soon be made which will obviate this handicap.

## ENTOMOLOGY

### J. G. Needham, Professor of Entomology

Courses in all the lines of work offered by the Department of Entomology were given during the year 1918–19, excepting apiculture. Due to the absence of Professor E. R. King in the aviation service, the instruction in apiculture has been temporarily abandoned. The care and upkeep of the apiary and equipment are in charge of W. P. Alexander.

The Department has endeavored to take advantage of the lessened demand for teaching, incident to the war, by getting the collection and equipment into better shape for future use. One instructor and one assistant, for example, who would ordinarily have been occupied with teaching elementary courses, have spent practically their whole time during the year in work on the collection, and the assistant professor of systematic entomology, whose classes have been small, has given a far larger part of his own time to the collection than would ordinarily have been possible. Out of this there has come very great improvement in the availability of our illustrative material — a permanent improvement that will affect most of the work of the Department beneficially in years to come.

The research work of the Department, in spite of considerable diversion to meet the needs of the war, has been prosecuted vigorously. A number of investigations have been completed and published, especially in economic lines, by Professors Herrick and Matheson and by Messrs. Muesebeck and Detwiler, and in aquicultural lines by Dr. Embody. Several important textbooks in preparation by members of the staff are nearing completion. The entomological work of the bean laboratory at Perry, New York, has been carried on by Dr. I. M. Hawley, and much good work has been done on the insects that interfere with the production of a bean crop.

The amount of research by graduate students has been somewhat less than usual, due to the entering of most of the students into the national service. Those who have remained, however, have accomplished much

good work. The enrollment of graduate students in this Department for the year is 24, a larger proportion than usual being women.

*Recommendations.*— As a general policy the research work in which the Department is engaged should be given the fullest possible support. Teaching is the part of our work that will always be taken care of first, because the students are on the ground. Extension has been provided for by government support more adequately than has anything else. In the long run, research is basic to both these activities. It is easy to find young men of good training, who are eager to work on subjects that have an economic bearing and who are willing to work for a mere living while getting advanced training, to come to Cornell and do research work. In the writer's judgment it would help the cause of the College, it would help production in New York State, it would help these young men who want the training, and it would help the student body at large, if some provision were made whereby such promising young men could be brought into the Department and kept going for a few years while studying some of the fundamental problems underlying better methods of insect control. It is the opportunity offered for advanced training and for obtaining a doctor's degree from the University, that would make it possible to get such young men here. Something like industrial fellowships, but maintained by the State and consequently a little freer from bias as to the direction that the work shall take, is what the writer has in mind. And such fellowships, in order to justify state support, should fall in the fields concerned with production within the State, providing for studies of insects affecting fruits, vegetable crops, forage crops, and livestock, of apiculture, of insects and other organisms that are important as food of fishes, of modes of increase of the fish food supply, and so forth.

Specific needs of the Department already familiar and reiterated are: a new building with more room for work and especially with better protection for the extremely valuable collections and library of the Department; a fish-cultural experiment station, where the work for which the Department has been preparing these many years may be carried forward; an apiary adequate for the work in teaching, the demand for which was unceasing even in war time, is bound to increase, and is going to be recognized by the beekeeping interests of the State and supported by them in the future.

It is recommended that as soon as possible a full-time helper for Dr. Allen in extension work in ornithology and mammalogy be appointed, and that a beginning be made in providing extension work in aquiculture. Pond culture is a rapidly growing interest in the State, and those who are beginning production in this field are entitled to more support in their work than we are at present able to give them.

## DAIRY INDUSTRY

### W. A. Stocking, Professor of Dairy Industry

During the past two or three years there have been marked changes in the dairy industry in New York State. Market milk, condensed and powdered milk, and ice cream, have assumed greater importance in relation to butter and cheese. These changes place new demands on the Department of Dairy Industry in its teaching and research work. The present Dairy Building is far too small to meet the Department's needs, and it is inadequate in design and equipment. The instruction in some courses is limited by the capacity of the laboratories. It is imperative that the Department should give instruction in every phase of dairy work. Equipment is especially needed for work in condensed milk, powdered milk, and dairy by-products such as casein, milk sugar, and the like.

As the result of the changes in dairy conditions in the State, mentioned above, demand has arisen also for plans for new dairy plants, and this Department has assisted in the preparation of both plans and equipment for plants in several sections. This work has been based on the special needs of the communities concerned.

The shortage of ice in New York State during the past winter has created an unusual need for work in connection with the keeping quality of market milk. A special effort is being made by the Department to meet this emergency so far as its limited facilities will permit. One of the greatest needs of the Department is for a well-trained man for extension work in market-milk problems.

## ANIMAL HUSBANDRY

### H. H. Wing, Professor of Animal Husbandry

Teaching, in the Department of Animal Husbandry, was almost entirely in abeyance from October 1, 1918, to January 1, 1919, because of the interference due to the work of the Student Army Training Corps. Since the latter date the enrollment in the Department has been about two-thirds normal.

The general lines of investigation in animal nutrition and animal statistics have been prosecuted and progress is being continually made. Some material is now awaiting publication.

The extension activities have been fully up to normal during the year and the work is continually growing. The chief lines of extension instruction are concerned with dairy cattle and nutrition of cows, but the renewed interest in sheep that began with the war has been maintained, and there seems to be an increasing demand for information and instruction with respect to swine and to beef cattle.

## POULTRY HUSBANDRY

### J. E. Rice, Professor of Poultry Husbandry

*Administration.*— Seven members of the staff of the Department of Poultry Husbandry were engaged in military service during the war.

The inventoried value of the property under the direct supervision of the Department, exclusive of the Cornell game farm, is as follows:

| | |
|---|---|
| Land (poultry farm, 30 acres owned, 50 acres rented; poultry instruction plant, approximately 2 acres; total, 82 acres) valued at approximately | $ 8,400.00 |
| Buildings | 119,465.00 |
| Stock | 3,057.00 |
| Equipment | 26,914.41 |
| Total | $157,836.41 |

The inventoried value of the Cornell game farm is as follows:

| | |
|---|---|
| Land (approximately 166 acres) | $9,200.00 |
| Buildings | 4,000.00 |
| Stock | 3,331.50 |
| Equipment | 6,361.00 |
| Total | $22,892.50 |

The total value of land, buildings, stock, and equipment of the poultry farm and the game farm is:

| | |
|---|---|
| Land, 248 acres | $ 17,600.00 |
| Buildings | 123,465.00 |
| Stock | 6,388.50 |
| Equipment | 33,275.41 |
| Total | $180,728.91 |

The kinds and amounts of poultry and game stock are as follows:

Poultry stock

| | |
|---|---|
| Poultry | 1,932 |
| Chicks | 2,700 |
| Ducks | 4 |
| Geese | 7 |
| Pigeons | 50 |
| Total | 4,693 |

| Game stock | Old | Young |
|---|---|---|
| Ring-necked pheasants | 350 | 650 |
| Golden pheasants | 11 | ..... |
| Silver pheasants | 18 | 10 |
| Quail | 10 | ..... |
| Canada geese | 8 | 3 |
| Wood duck | 1 | ..... |
| Wild mallard ducks | 24 | 33 |
| Black ducks | 2 | ..... |
| Domestic fowl | 400 | ..... |
| Bantams | 40 | ..... |
| Total | 1,560 | |

The income from poultry sales in the Department during the year was $9495.52; that from the game farm was $274; making a total of $9769.52. Two hundred and forty cock pheasants valued at $5 each, or a total value of $1200, were turned over to the State Conservation Commission for distribution.

Great improvement has been made on the poultry farm during the year. Two large commercial units were constructed by military-service vocational students under the direction of Sibley College, the poultry houses were painted, and the walks were considerably improved. On the game farm the residence and the barns are being completely overhauled and put into first-class condition. A large amount of land drainage has been effected, fences have been built around the large rearing range, and a large number of coops and rearing pens have been constructed; so that at the end of the first year the game farm is well organized, well stocked, and equipped to handle the present amount of stock.

Through the hearty cooperation of the Department of Rural Engineering, the Department of Forestry, and the Department of Landscape Art, a comprehensive survey and plan of the poultry farm and the game farm has been made. The plan provides for extensive plantings for shelter, shade, and landscape effect, for adequate drainage systems, and for the construction of a waterfowl sanctuary and breeding ponds to be completed under the special appropriation by the Legislature of $3400 to be expended during the next fiscal year.

*Teaching.*— The total number of students taking regular courses in poultry husbandry in 1918–19, including the winter course and the summer school, was 159.

The figures for the first annual Cornell judging and breeding school held July 1 to 6, 1918, are as follows:

| | Students | Nonresident staff | Resident staff |
|---|---|---|---|
| Teachers, investigators, and extension specialists | 14 | 7 | 9 |
| Poultrymen | 9 | ..... | ..... |
| Editors | 1 | ..... | ..... |
| Judges | ..... | 5 | ..... |
| Others | 3 | ..... | ..... |
| Total | 27 | 12 | 9 |

Grand total, 48, representing ten States, the District of Columbia, and Canada.

*Research.*— The following problems are being studied by the Department.

1. Inheritance of fecundity. In this study, which has been in progress for six years, an attempt is being made to discover and establish some of the laws governing the inheritance of egg production in the domestic fowl. Two lines are being developed, a high line and a low line, by pedigree breeding and stud mating, and to study the effect of the direct and the reciprocal cross of the two lines.

2. Distribution of egg production. This investigation has been in progress for ten years. Studies are being made of trap-nest records of birds in various experiment projects, to determine the manner and the time of ovulation as influenced by climate, temperature, sunlight, artificial light, methods of feeding and housing, age, time of hatching, breed, variety, strain, and individual characteristics.

3. Relation of physical characters to egg production. In this investigation, which has been in progress for nine years, weekly and monthly measurements are being made of the various sections of the body of the fowl. Observations are frequently made also of color characters, shanks, ear lobes, skin, plumage, texture of comb, time of molt, sequence of molt, actions, and other factors.

4. In-breeding. This study has been under way for four years. In the " in-bred line," brother-and-sister matings are continued each year. In the " out-cross line," new blood is brought in each year. Direct and reciprocal crosses are made each year, and this process is continued.

5. Inheritance of size, shape, and color of eggs. This is a comparative study of egg types, which has been in progress for seven years. It involves the use of nearly six hundred trap-nested hens and a large number of their pedigreed offspring. The object is to determine to what extent egg characters of size, shape, and color are transmissible.

6. Development of body characters by continuous selection of the most advanced types. This study has been in progress for four years. Matings and selections are made of fowls showing variation in normal characters,

such, for example, as buff in white birds, white in mottled birds, red earlobes in white-ear-lobed birds, feathered shanks in non-feathered-shank varieties, silky plumage in plain-plumaged birds, and the like.

7. Development and behavior of males as an indication of breeding value. This is a study of the relationship existing between rate of development, size, color, comb, shank, and other characters; and also of the relationship between primary and secondary sexual characters, behavior, constitutional vigor, and other characteristics, and mating qualities and power of transmission of vitality and fecundity.

8. Inheritance of comb type. In this investigation, observations are being made of the results of crosses and outcrossing of strains of the same variety, on variation in comb type.

9. Comparison of breeds and varieties for egg production. This is a study of breed characteristics as influencing the number and quality of eggs laid.

10. Relation between pigmentation of parents and the hatching quality of eggs. This is a study of the possible relationship between color pigmentation, as an indication of vitality to be transmitted to offspring, and the fertility and hatching power of eggs.

11. Comparison of various methods of feeding the Cornell ration to pullets for egg production.

12. Comparison of varying amounts and sources of animal protein. Various animal feeds, such as meat scrap, fish, milk, tankage, and high- and low-fiber rations, are compared as to their effect on egg production and its cost.

13. Comparison of methods of feeding hens for breeding purposes. This is a study of variation in kind of ration and method of feeding, to determine the influence on the number of eggs laid, the fertility and hatching power of the eggs, and the vigor of the chicks.

14. Effect of lengthening the day by means of artificial light, on development in respect to the feeding of young birds. This is a study of the influence of equalizing the time between meals, by shortening the period of darkness during the fall and winter months by means of artificial light.

15. Relation of the rate and method of digestion of feeds to egg production. In this study an attempt is being made to ascertain the comparative amount of time required for various kinds and conditions of food to be digested, and the results on egg production.

16. Methods of feeding for egg production under normal conditions of light. This investigation is undertaken for the purpose of ascertaining the changes that take place in the rapidity of digestion and assimilation of foods under natural conditions, as a basis for similar observations under the influence of artificial light as affecting egg production.

17. Influence of artificial light on egg production. This is a comparison of various amounts of artificial light at different times of the day and year, as influencing the number of eggs laid, the fertility and hatching power of the eggs, the vigor of the stock, mortality, cost of production, and other factors.

18. Factors influencing the temperature, composition, and humidity of the air, and the intensity of the light, of poultry houses under varying environmental conditions and methods of construction. In this study of factors influencing the efficiency of poultry buildings, a large model poultry house, especially designed to observe the factors under exact control, is being used.

19. Comparison of methods and systems of artificial illumination of poultry houses. This investigation has been undertaken in cooperation with the Department of Rural Engineering. It is a study of the efficiency of various devices for lighting poultry buildings artificially, with a view to increasing egg production.

20. Preservation of market eggs. Twenty methods of egg preservation, including cold storage for two seasons, are being compared by physical and bacteriological inspection of the eggs.

21. Determination of egg grades. This is a study of egg grades undertaken with a view to establishing market standards.

22. Causes of loss of eggs and poultry in transit. Eggs and poultry are inspected at the point of shipment and at the destination, in order to determine the extent of injury or loss in transit and the causes and remedies therefor.

23. Relative importance of temperature, humidity, and purity of the air, and of cooling and turning, on the hatching of eggs. This is a study of the exact conditions that obtain in the hatching of eggs under exact control conditions, with the object of determining the comparative importance of the various factors having to do with successful incubation.

From the foregoing it is seen that the Department has now under investigation, by various members of its staff, 23 projects. In these there are being used 2098 females, nearly all of which are trap-nested, and 202 males, or a total of 2300 fowls.

*Extension.*— The following table shows the principal extension activities of the Department for the year 1917–18 as compared to 1918–19:

| | 1917–18 | 1918–19 |
|---|---|---|
| Lectures and demonstrations | 594 | 548 |
| Educational exhibits | 66 | 124 |
| Farm visits | 227 | 178 |
| Attendance at meetings | 19,140 | 15,470 |

The figures for culling and selection campaigns for poultry improvement in the past three years are as follows:

| | 1916–17 | 1917–18 | 1918–19 | |
|---|---|---|---|---|
| Stock selected..... | 10,145 | 12,507 | 16,028 | |
| Fowls pledged for selection | 153,032 | 378,713 | 348,082 | |
| Fowls certified..... | ..... | ..... | 3,530 | (on approximately 50 farms in 20 counties) |

The certification project bids fair to be one of the most important pieces of extension work for poultry improvement which has yet been undertaken. It will require a larger staff than now appears to be available to adequately cover the culling and the certification work in the State during the months of July, August, September, October, and November, when the work must be done.

Extension projects undertaken in 1918–19 were as follows:

1. Culling out the low-producing hens. July, August, September.
2. Selection of cockerels to be kept for breeders. July, August, September, October.
3. Selection and color leg-banding of pullets according to quality. October, November, December, January.
4. Certification of breeders (males and females). October, November.
5. Supervised pedigree records and line breeding for production on the farm.
6. Distribution of Cornell pedigreed chicks. May.
7. Distribution of Cornell pedigreed cockerels. July, August.
8. Pedigree breeding of certified stock at the Cornell poultry proving station. Open to cooperators in projects 1, 2, 3, and 4.
9. Reorganization of poultry premium lists of agricultural fairs and poultry associations, to fit the communities and to judge the egg-laying classes. July, August, September.
10. Control of lice and mites. July, August.
11. Remodeling poultry houses. July, August, September, October.
12. Illumination to increase fall and winter production. October, November, December, January.
13. Demonstration in methods of feeding.
14. Killing, picking, and packing poultry.
15. Cost-account record-keeping.
16. Personally conducted excursions for farmers and poultrymen to study market conditions in New York City. February, March.

*Recommendations.*— The five pressing needs of the Department are:

1. The construction of buildings to complete the poultry plant in accordance with plans already prepared and submitted.

2. An increase in the departmental staff, to include an expert accountant. The services of such an accountant are almost indispensable for the proper handling of the records involved in the management of the large numbers of trap-nested birds used in the numerous research projects of the Department.

3. Suitable equipment for fundamental research work in the field of nutrition and incubation, in which individual egg and individual hen studies can be made only by the use of apparatus especially prepared for this purpose.

4. Special appropriations for drainage, grading, construction of walks and roads, and plantings, to beautify and to make accessible and effective the land and buildings of the Department.

5. If the Department is to compete with other institutions, and especially with commercial enterprises for men, it is imperatively necessary that salaries be materially increased. Some of the strongest men now engaged in poultry work in other institutions have very reluctantly entered the commercial field because salaries paid by educational institutions are such that they could not afford to continue in educational work. This is much to be regretted, since it is the men, rather than the land, buildings, or equipment, that make an institution. It would be exceedingly unfortunate if one or more persons on our staff should yield to the persuasive argument of a very much higher salary to go elsewhere. The last-named is the most important need of the Department.

Notwithstanding its urgent need for more buildings, equipment, and staff in order to meet the ever-pressing demands of the people of the State, the Department is in better condition to meet these responsibilities than it has ever been heretofore. We now have more and better buildings, a larger and better-trained staff, more and better stock, more equipment and general facilities, than at any previous time in the history of the College.

## RURAL ENGINEERING

### H. W. Riley, Professor of Rural Engineering

*Teaching.*— The general course in mechanics was not given by the Department of Rural Engineering in the second semester of the year 1918–19. This made it possible for the Department to offer two special tractor schools which were not open to students in the University. As the regular laboratory equipment could be stored to make room for the equipment necessary for this teaching, the entire laboratory floor space was available for this work. The New York State Food Commission stored eighteen of its tractors in Ithaca and allowed our students to overhaul

them and make necessary repairs in the laboratory. This condition contributed materially to making these schools possible.

The tractor schools were each of three weeks duration, but many of the students in each school were so interested and so anxious to get all they could that they remained an extra week. In the first school there were 24 students, and in the second 41. Many applicants were refused admission because of lack of room.

So keen is the interest in farm tractors at this time that the regular students in the College of Agriculture presented a petition asking this Department to offer a course in tractors during the spring term, and at the request of the Dean such a course was offered. The fact that laboratory apparatus was provided in five tractors donated to the College by the New York State Food Commission, and that laboratory space and necessary instructors were made available by the temporary discontinuance of the regular course in dairy mechanics, contributed to make this course possible.

*Extension.*— The continued shortage of farm labor and the abnormally high prices of farm products have greatly encouraged the more general use of complicated types of farm machinery. The machine that is most rapidly coming into general use is the gas engine, which is used both for stationary work and as a power plant in tractors, farm trucks, and farm automobiles. Farmers are realizing more and more that the best results with their machinery are obtainable only when the different mechanisms are well understood. Especially is this true with the gas engine.

The tractor schools, so successfully started and conducted a year ago by the New York State Food Commission, were continued this past winter. These schools furnished one of the best examples known of cooperation in extension teaching, being a cooperative enterprise between the New York State Food Commission, the farm bureaus, the tractor manufacturers, and the Department of Rural Engineering of the College. The Food Commission made the general arrangements and provided the funds; the farm bureaus attended to local details; the tractor companies furnished the tractors and the mechanical or laboratory instructors; and this Department assumed the active administration of the schools. Twenty-one schools were held this past year, the first one on December 2 and the last on March 4. The total enrollment was 1131, the average attendance 54; of those attending, 83 per cent were farmers, 311 were tractor owners, and 779 attended every session. At most of these schools a special evening session was held, at which rope splicing and belt lacing were taught.

In the winter two new types of extension schools were started — milking-machine schools and farm-mechanics schools. The former, in

cooperation with the Department of Dairy Industry, took up the subject of gas engines and milking machines, their care and operation. The latter dealt with gas engines with relation to some other phases of mechanics, and with water supply, sewage-disposal systems, rope splicing, pipe fitting, and the like. These schools seemed to meet the needs of the farmers who attended them, and it is believed that they will be a popular type of extension school from this Department in the near future.

The New York State Food Commission had in the field this year, under the jurisdiction of the different county agents, thirteen power ditching machines. The Commission, as previously, turned to the College of Agriculture for assistance in the technical administration of these machines. Various members of this Department spent a large part of their time in laying out drainage systems and conducting demonstrations with the machines. Not only was this a most valuable piece of extension work, but its industrial importance is considerable. There were actually constructed by this means nearly 40,000 rods of underdrains which otherwise would probably not have been put in.

In addition to the work with the ditching machines, the Department has carried on a considerable amount of extension work in especially difficult drainage demonstrations. Members of the Department have also been called in to advise as to the best method of draining several large muck areas.

*Recommendations.*— The prospect of securing additional space for a tractor laboratory and a small wood shop and instructor's office in the new temporary building merely serves to emphasize the great need of this Department for really adequate quarters. The war has emphasized with renewed force the importance of engineering in present-day agriculture, and it is clearly the duty of the State to see to it that adequate quarters for the teaching of so important a division be provided in the very near future.

## AGRICULTURAL CHEMISTRY

G. W. Cavanaugh, Professor of Chemistry in its Relations to Agriculture

The Department of Agricultural Chemistry continues to be severely handicapped because of lack of space and equipment since fire destroyed the chemistry building. It is disadvantaged also by the fact that its work is given in two widely separated buildings.

While teaching necessarily absorbs the major attention of members of the staff, certain investigations have been carried forward. Among these is a study of the decomposition of butterfat, with special reference to the keeping qualities of the product. This work is under the supervision of the head of the Department. The Department has also installed, jointly with

the Department of Botany, an apparatus for the electrometric determination of hydrogen ion concentration. Studies are being made on the use of this apparatus in measuring the hydrogen ion concentration of milk, soil solutions, plant juices, and other materials. Research in the chemical and physical composition and properties of milk is being conducted by Assistant Professor Rice. Professor Cross has under study the dehydration of certain vegetables, the preparation of the vegetable flours, and the manufacture of concentrated soups. Research dealing with the fruit juices is also being carried on by him, as well as certain problems connected with the milk industry.

Since July, 1918, the extension laboratory of the Department has received 388 samples of miscellaneous products for chemical analysis. These samples have been received chiefly through the county agricultural agents, but some have come directly from many of the farmers of the State. They consist of soils, fertilizers, feeds, limestones, insecticides, and vinegars and various other food products. When a chemical analysis is made and reported to the sender, the Department has adopted the practice of informing the county agent of the results. This is in conformity with the practice of making the farm bureaus the local clearing houses for work in their communities.

## LANDSCAPE ART

E. G. Davis, R. W. Curtis, Professors of Landscape Art

*Teaching.*— The instruction given in the Department of Landscape Art is both general and technical, and is planned to meet the needs of three classes of students, as follows:

1. Students in the College of Agriculture or in other colleges of the University who desire a better general understanding of the fundamental principles of landscape architecture and gardening. For such students the Department offers several courses designed to foster an appreciation of landscape work in general, and an understanding of the basic principles governing the arrangement, adaptation, and beautification of land for human use and enjoyment. These courses include a review of the history of landscape achievements, an introduction to the plant materials used, and an exposition of the elementary principles of landscape planning.

2. Students in technical courses in this or other colleges of the University whose work is allied to landscape art and who wish a better understanding of such principles of landscape design as relate to their particular field of work.

3. Professional students in landscape art. For this group of students the Department maintains a professional school of landscape architecture,

the purpose of which is twofold — to produce a few students well trained for the practice of landscape architecture, and to serve as a means of developing theories, principles, methods, and ideals essential to progress and improvement in both teaching and extension work in landscape art. Landscape architecture, being an applied art, must be taught as such. As this art builds upon natural conditions of the ground and vegetation, an understanding of natural science is essential, and art and the artificial are not allowed to overshadow natural science in the professional study of landscape architecture.

The following comparison of enrollments (not counting duplicates) is of interest:

1907–08, 12 (in technical courses).
1911–12, 17 in technical courses, 25 in general courses.
1916–17, 32 in technical courses, 414 in general courses.

Space for technical students in the Department's drafting room is limited to 35, including postgraduates. Most of the students in general courses have been from the College of Agriculture, but other colleges have been represented in the following order: Architecture, Arts and Sciences, Civil Engineering, Mechanical Engineering. This comparison indicates a growing and rather widespread interest in landscape architecture among university students.

*Extension.*— The Department now has facilities for giving consecutive attention to extension work. The motive in this field is to improve the landscape conditions of the rural home, school, and village, and to enchance the value of farm properties by improved arrangements of buildings and grounds and by more attractive plantings of trees, shrubs, and vines. While the first interest is the improvement of home grounds on the farm and in the village, yet there are other features which contribute to the landscape setting of the home and which influence the living conditions. Some of these contributory features which must receive attention are the highways, railroad and barge-canal systems, schools and churches, fair grounds and other public and semi-public institutions, state reservations, community centers, parks and playgrounds, and streets and street equipment.

On the request of county agricultural agents, school supervisors, village improvement societies, and individuals, visits to communities have been arranged, illustrated lectures given, and data taken from which plans and recommendations have been prepared. Correspondence and later visits have followed up this interest in local improvement. It is planned to undertake a limited number of demonstrations of arrangement, grading,

and planting, where the finished results will serve as an example for the community.

The survey to gather data on the actual plans of arrangement of New York State farms has been continued and is proving invaluable. Surveys of rural school grounds and of country roads are also being made.

## RURAL ECONOMY

### G. N. Lauman, Professor of Rural Economy

The study of cooperative marketing efforts in the Chautauqua-Erie grape industry undertaken by H. D. Phillips, until recently an instructor in the Department of Rural Economy, has been completed and the results are ready for publication. Professor Boyle has completed a bulletin on the distribution of the western New York peach crop, based primarily on the original railroad records, which should be of service to peach growers and shippers. Another bulletin nearly ready for publication, which will answer many questions now answered by letter, deals with the farm credit situation in New York.

Efforts to fill the position of investigator in marketing provided for in the budget have not been successful, due to the demands of war work and the limited salary available.

The extension activities of the Department have been in the hands of Professor James E. Boyle since October 1, 1918. His reception in the State among farmers as well as business men augurs well for the future in a field full of peculiar difficulties and pitfalls. The value of a fundamental plan for extension work such as the Department has prepared was seen in the proposal to add to the departmental staff a rural transportation specialist, a recommendation arrived at by a regional committee affiliated with the National Council of Defense.

## RURAL EDUCATION

### G. A. Works, Professor of Rural Education

*Teaching.*— The passage of the Smith-Hughes Act has stimulated the demand for state supervisors of vocational agriculture and for men to engage in the professional preparation of secondary-school teachers of vocational agriculture. This has given the Department of Rural Education an opportunity to render a needed service by expanding its instructional work to assist persons desiring to better equip themselves for these fields. Courses were offered for the first time in the Summer Session of 1918. The need for the work was shown by the fact that attending these courses were men from New York State, Mississippi,

South Carolina, North Carolina, New Jersey, Pennsylvania, Iowa, and Nebraska. The continuance of the work during the regular academic year has resulted in enrollments from Virginia, New York, Vermont, Missouri, North Carolina, Iowa, and Texas.

The war so depleted the available supply of teachers of vocational agriculture for the high schools of the State, that it seemed necessary, unless many of the high-school departments of vocational agriculture were to be discontinued, that men who were not liable to call for military service should be engaged. At the request of the State Department of Education and with the cooperation of the Division of Agricultural and Industrial Education, an emergency course, nine weeks in length, was offered. Eighteen selected men were admitted to instruction and given an intensive course. This made available a sufficient number of men so that it was possible to keep open most of the departments of agriculture in the high schools of the State.

The enrollment in the summer school remained nearly normal in spite of the war. That this condition obtained was due largely to the fact that courses in physical education were added to the work available. In the 1918 session there were approximately 150 students devoting their entire time to these courses. There is no question that this work has filled a real need in supplying teachers for service in the public schools. The demand which this instruction has made on the financial resources of the summer is so great that it has been impossible to adequately develop other phases. It seems imperative to either abandon the work or provide a larger fund for the summer school.

*Extension.*— The junior extension work has had a rapid growth during the past season, due partly to the stimulation of the war demand for foodstuffs and the war emergency appropriation therefor. There were regularly enrolled during the year ending December 1, 1918, a total of 23,444 project workers. Of these, 18,003 completed their project work, and, according to their reports, produced food products to the value of $140,877.50. These project workers were distributed in every county in the State outside of New York City, with one exception. In all cases this work was done in cooperation with the schools, and, in addition to the regular school officials and teachers, twenty county leaders and assistant county leaders were employed.

Enrollment for the present season began on January 1. Up to the present time 19,378 new enrollments have been received. An effort is being made this year to organize the work on a systematic basis and to place the responsibility in the several counties on county junior extension boards or on committees representing the educational, agricultural, and

home-making interests of the counties. At the present time eighteen counties have been so organized and fourteen county-wide leaders have been employed.

Past experience shows that in order to be successful this work must be conscientiously supervised. An effort is being made to engage local leaders or supervisors in those counties that have not yet been fully organized. In several counties the boards of supervisors stand ready to make special appropriations for carrying on the work as soon as some means can be found to legalize the appropriation of county funds to the county boards of junior extension for this purpose.

The resignation of Assistant Professor E. M. Tuttle made it necessary to greatly reduce the extension activities associated with the Cornell Rural School Leaflet. Professor R. M. Stewart was released from teaching for the first term of the regular year to take charge of this work. It is hoped that by another year it may be possible to have a member of the staff devoting his entire time to the Leaflet in order to develop it in so far as printing funds will permit. The repeated calls from teachers and superintendents indicate that they feel the need for this publication.

*Research.*— At the request of the school authorities in Livingston County, the Department has been cooperating with them in a study of the rural schools of that county. This work has been in progress for nearly two years. The results of the study are practically ready for printing.

At the request of the Federal Board for Vocational Education, Professor Lusk has undertaken a study of the use of land in connection with the teaching of agriculture in secondary schools.

*Recommendations.*— The library facilities for advanced students are inadequate. There is a decided need for additional books and magazines covering the field of education.

The quarters of the Department have become so crowded that it will be necessary to have more space in the near future.

The demand for admission to courses 1 and 2 is so great that the restrictions now obtaining because these courses are given on Smith-Hughes funds should be removed. This can be done only when the State makes a larger provision for this work.

The staff of the Department should be strengthened by the addition of a strong man in elementary education. In the initial stages his work might well be confined largely to extension, but in the near future the Department should be ready to assist in the preparation of rural-school supervisors.

## RURAL ORGANIZATION

Dwight Sanderson, Professor of Rural Organization

This being the first year for the new Department of Rural Organization, but one course was offered. This was given in the third term and repeated in the summer term and the summer school.

No systematic extension work has been done by the Department, but the writer has made several addresses before granges, grange conferences, and community organizations. A definite series of projects for extension work in rural organization has been drawn up and approved. Without a specialist who can devote his time to such work, it does not seem advisable to push extension activities.

The writer spent a fortnight in making a study of one rural community, and in the third term Dr. Warren S. Thompson spent most of his time in the field studying four communities in Monroe County. The data gathered are now being studied. As time permits, such studies will be continued in some of the more successful rural communities in the State, until sufficient data have been gathered to warrant making conclusions and generalizations.

*Recommendations.*— The American Red Cross, with the cooperation of the New York School of Social Work, has submitted a proposition for a one-year course of training for home service workers, the first half of which will be given by the New York school and the second half by this institution. If this work is undertaken, the Department should have an assistant professor for teaching social case work in the rural family. The Red Cross is willing to pay the salary of such a teacher for the first semester, during which the teacher could assemble material for such instruction, possibly visiting some parts of the country; and the Red Cross is willing to pay one-half of the salary during the second semester, when the course will be given here, the College paying the other half to the amount of $500, making a total salary of $2000 for nine months. If this plan is carried out, the position should be made a permanent assistant professorship at a salary of $2500, to be paid in full by this institution.

The most important need of the work in rural organization, as a basis both of teaching and of extension work, is the largest possible amount of personal investigation of the social organization of rural communities. It is not possible to make these field investigations at odd times. They require continued presence in the field. If the institution is to undertake a definite policy in promoting better social conditions of rural life, it seems imperative that these conditions should be given as careful investigation as has been given to other fields of agricultural science.

There is a very evident need and desire for extension work in community organization and in the promotion of rural recreation. In the progress of such work, much valuable information and experience will be gathered which could not be obtained otherwise, even through a definite investigation project. We should as soon as possible employ a man to give his full time to this work.

## HOME ECONOMICS

Martha Van Rensselaer, Flora Rose, Professors of Home Economics

The work of the Department of Home Economics has been largely determined during this year, as during the other years of the war, by the changing living conditions.

Because of the development and strengthening of the teaching courses, and because of the added extension work, the staff membership has been considerably increased during the past few years. Assistants and student assistants have been largely eliminated from the teaching staff, and experienced and well-trained instructors have been substituted. This change and the reduction in the size of the laboratory sections have brought the courses offered to a high standard. Instructors have been added this year in the courses in foods and clothing, and the entire time of one instructor is devoted to the work in institution management. During the period of the war, each member of the teaching staff had to help in the preparation of subject matter for extension work.

It is gratifying to note that the registration of regular students did not decrease materially during the war period. A growing number of requests seems to indicate a demand for winter courses giving more technical subject matter and offering college credit.

*Teaching.*— In the regular teaching work, two new courses have been added this year: one in the freshman class, to introduce entering students to the study of foods; and one for seniors, to give them some instruction in abnormal nutrition from the standpoint of the hospitals. The content of the courses has been changed, bringing about a closer relation of each course to others in the curriculum. A storeroom for the work in foods has been organized to simplify laboratory service.

A class in dietetics has been taught in the Ithaca City Hospital, and students have worked on cases with the Associated Charities.

Because the entire time of one instructor has been devoted to teaching institution management, it has been possible to increase the content of the courses. Students have obtained practice regularly in the Home Economics cafeteria, and occasionally at the Forest Home tea room. Arrangements have been made for practice in dormitory housekeeping

in the women's residential halls. Whenever opportunity has offered, the students have gained experience in serving large numbers of persons.

A small emergency cafeteria was opened on the second floor of the Home Economics Building while the United States Government was using the cafeteria for the Student Army Training Corps. All the work connected with the temporary cafeteria was done by students.

During the epidemic of influenza, students assisted in the diet kitchens of the Cornell Infirmary.

The study of the arrangement and plan of dwellings has been closely connected with their decoration and furnishing. Much time has been spent on the problems of industrial housing, as well as on the problems of housing in country, town, and city. The Home Economics Lodge has been improved and furnished to illustrate the principles taught in these courses.

The course in extension in home economics has been constantly adapted as experience in the field has furnished new aspects of extension service. The war emergency emphasized the need for special training for this group of workers. It is probable that this course should be developed into a graduate course open only to graduate students with several years of experience. Undergraduates are too immature for extension positions, and at present there is a limited field for apprentices.

*Extension.*— With the restoration of normal conditions after the war, there has been a reorganization of the extension work of the Department. One of the heads of the Department has been placed in charge of the state service in home economics extension, and the State Leader and Assistant State Leaders of Home Demonstration Agents have been added to the Department. Thus the Department has become a unit for home economics extension activities, under the Director and the Vice Director of Extension.

The extension work during the past year has been adapted to meet the changed situation caused by the war and the signing of the armistice. Requests from the field since January indicate a return to pre-war conditions. Whereas the emphasis until November was primarily centered on food conservation, since that time the demand has been rather for work on clothing, civics, nutrition, and health.

During the winter the extension specialists have cooperated with the home bureaus in starting home-economics projects. The work that has been done in the organized counties includes projects in thrift, clothing, millinery, civics, health and home nursing, school lunches, the use of milk in the home, the care and feeding of children, and community enterprises such as canning kitchens and cooked-food centers.

Since July 1, 1918, there have been held 361 community meetings, including lectures and demonstrations, with an attendance of 24,236. Of these meetings, 26 were at farmers' institutes. In addition to these meetings on subject matter, 28 meetings on organization were held, with an attendance of 788. The majority of these organization meetings were held in Chautauqua and Cattaraugus Counties through the co-operation of the United States Food Administration, for the purpose of establishing a temporary channel for quick distribution of information and printed matter on food conservation and ultimately changing this to a permanent organization of women for work in home economics.

During the year 61 conferences have been attended. Meetings of executive committees and advisory councils of the home bureau, as well as of miscellaneous committees, are included.

Since January a few requests for two-days extension schools have been received, indicating a return to pre-war conditions. Three schools in foods and three in clothing have been held, with a total enrollment of 190.

The "Victory Special," consisting of two railway coaches fitted up for demonstrations, lectures, and exhibits, toured the State over the New York Central, the Long Island, the Delaware, Lackawanna and Western, and the Delaware and Hudson Railroad, from May 9 to October 19, 1918. After July 1, stops were made in 78 places in 29 counties. About 10,121 persons visited the cars. The "Victory Special" left Ithaca on April 27, 1919, for the work of this season. It is being operated over the lines of the New York Central, the Lehigh Valley, the Ontario and Western, the Delaware, Lackawanna and Western, the Delaware and Hudson, the Erie, the Rutland, and the Fonda, Johnstown and Gloversville. The schedule includes 120 meetings between April 29 and October 3; 45 meetings were held up to June 30, with a total attendance of 5407.

The preparation of lessons in the Cornell Reading Course for the Farm Home was somewhat interrupted by the emergency publications which the Department prepared for the New York State Food Commission. These emergency circulars were not distributed to the mailing list for the reading-course lessons, but were used to fill individual requests and were distributed by the home demonstration agents in their counties. They were:

Save sugar and save fruit.
What to do with beans.
The Victory wheat plan.
War-winning menus and recipes, I, II, III, IV. (Prepared for the State Fair.)

The number of persons enrolled to receive the lessons in the Cornell Reading Course for the Farm Home is 70,085, which is an increase of

8930 since July 1, 1918. There have been 10,860 individual requests for lessons, of which 2633 were from persons outside the State. Many requests were for emergency material and were answered by the circulars issued in cooperation with the New York State Food Commission. A record of such requests was not included in the departmental records, since distribution was made through the Food Commission. Eleven lessons were published in the Cornell Reading Course for the Farm Home.

On March 1, 1919, there were listed on the departmental records 271 Cornell study clubs. Because of pressure of work and the limited staff, it was impossible for the Department to maintain during the war as close a relationship with the clubs as had previously been possible. Now, however, the full time of one member of the staff is being given to cooperation with the clubs. On March 12 a letter was sent to each club asking whether the club was to be maintained and whether assistance with programs was desired. Sixty-eight clubs replied. The answers indicated that the majority of the clubs replying had turned their organized efforts to Red Cross or other war work, and are now desirous of returning to the definite study of home economics or community work.

Eighteen club programs were prepared by the Department during the year. In the summer and fall of 1918, while the need for food conservation was pressing, programs and printed material were supplied for monthly meetings. Thrift was emphasized during the winter and spring, and a reading-course lesson containing club programs on thrift was published. Six programs on home nursing were also prepared.

The food exhibit at the State Fair at Syracuse was prepared with the purpose of emphasizing to the public the fact that palatable dishes could be made from the substitutes which the United States Food Administration was asking the people to use. As an example of conservation, all the food prepared in the demonstrations or for the exhibits was used in some way. Demonstrations on wheat-saving yeast breads and quick breads, meat-saving dishes, and sugar-saving dishes, were given from nine to five o'clock daily. The demonstrations were given by housewives of the State who volunteered their services. Home demonstration agents from several counties assisted. Sample dishes of the food prepared at the demonstration tables were on exhibition in glass show cases. At the end of each day these were given out in small portions to the public. A conservation dinner was served each day to from 150 to 200 persons. The menus and recipes were available in printed form. Each afternoon, from twenty to sixty children were served with sample dairy suppers consisting of the milk dishes prepared by the demonstrators. Extension specialists were present to answer questions, and about 74,000 publications were distributed.

Two exhibits were prepared for county fairs with the cooperation of the New York State Food Commission. One large exhibit was sent to six fairs, and three duplicates of a small exhibit were sent to fifteen fairs.

At the milk show held in Elmira on January 9 and 10 through the cooperation of the local board of health, milk dealers, Holstein breeders, and the State College of Agriculture, the Department of Home Economics planned and helped to prepare exhibits showing the value of milk as compared with other foods, and simple milk dishes. Groups of children were served milk meals in a store window where the attention of the public was attracted. Milk was served free each day to children attending the milk show.

At the Second National Farm and Dairy Exposition held in New York City April 21 to 26, the Department had charge of one booth. Exhibits showed the food value of milk as compared with certain other foods, meals in which milk was liberally used, and unusual milk dishes. The making of simple milk dishes was demonstrated by housekeepers from various parts of the State. During the week 40,000 penny portions of milk dishes were sold. Two leaflets, entitled *Ways of Using Milk* and *Answers to Questions about Milk*, respectively, were prepared by the Department for distribution.

The emergency publicity work begun in the preceding year was continued until December. News material from the United States Food Administration was sent out from the Department through the cooperation of the College and the Conservation Bureau of the New York State Food Commission. The material was issued in weekly or bi-weekly bulletins to county home demonstration agents, county agricultural agents, and federal food deputies.

"Victory Menus," a series of conservation menus and recipes for each day in the week, were prepared by the Department and issued by the New York State Food Commission through the newspapers of the State.

The first two days of Farmers' Week, this Department cooperated with the Department of Rural Organization in a program on the rural community. The remaining days of the week were given over to lectures, demonstrations, and conferences on home economics. During the week 635 women registered in the Home Economics Building. The outstanding features in the Home-makers' Conference this year was Women's Organization Day, when an attempt was made to bring together the women of the leading organizations of the State in order that both rural and urban women might appreciate the value of organization among women and learn of the plans for reconstruction proposed by these social forces. Exhibits during the week showed wise and unwise selection

of food, the menace of patent medicines, preserved foods, wild foods that are good to eat, fireless and steam-pressure cookers, dishes made from preserved fish, food and fuel waste, clothing and millinery, care of children, school lunches, health, house plans and interiors, books and bulletins for club study.

For the junior extension work in home economics two subject-matter specialists are employed for full time. These specialists are members of the Department. They spend about one-half time in the field working with district superintendents and various other local leaders in junior extension work. Since July 1, 1918, there have been held 98 general meetings with an attendance of 5564, and 47 conferences with an attendance of 269. Manuals of instruction have been prepared for the children registered for project work in foods and clothing. Two of these, *First Lessons in Sewing* and *Elementary Garment Making*, are printed and in use. The one for the work in foods is in manuscript form. To supplement this material, which is mailed direct to the workers, special circulars are sent to the teachers who are local leaders of the projects. These contain seasonal suggestions as to the methods of using the subject-matter material. Previous to September 1, 1918, there were 4066 girls registered for this work. From September 1, 1918, to June 30,1919, there were 6669 registered, making a total of 10,735.

*Research.*— A canning kitchen was opened in the basement of the Home Economics Building in the summer, for use by the campus community. The purpose was not only to provide a place where the women of the neighborhood might do their canning, but also to discover by careful observation and records whether such a kitchen was an economical and desirable undertaking, and to study types and arrangement of equipment. The canning was done both for home use and for sale for philanthropic work, certain days being given over for each purpose. More than one hundred university families were represented in the service of the kitchen. Twenty-nine women gave regular volunteer help during the season. During the four months in which the kitchen was in operation, the average daily attendance for individual work was $6\frac{1}{2}$; that for philanthropic work was $9\frac{3}{4}$. The number of jars of food preserved was 5316.

In the course in household management, an investigation has been conducted to determine the necessary readjustment of the household budget to fit the changing cost of food, housing, and clothing, and maintain the efficiency of the family.

*Cafeteria and laundry.*— The regulations of the United States Food Administration were closely followed in the cafeteria while they were in force. Corn bread and quick bread were substituted for whole wheat

bread, and all the wheat flour in stock was released for other purposes. Wheat flour substitutes were used entirely in the cafeteria service.

When the Student Army Training Corps was organized at Cornell, the United States Government requested that the dining-rooms on the campus be used as mess halls to curtail building expenses. The cafeteria was used as a mess hall under the management of the Department of Home Economics from October 10 to December 14, when the S. A. T. C. was disbanded. As the university dining-rooms could serve only 500 soldiers, the remaining 900 were served in the Home Economics cafeteria. This dining-room has a seating capacity of 640, and it was necessary to serve six meals daily. The two seatings were put through in 65 minutes. To reset the tables for the second seating and still keep within the time limit required careful planning and concentrated effort.

In addition to the cafeteria and mess-hall management, an experimental community laundry has been organized in the Dairy Building by the manager of the cafeteria.

*Recommendations.*— It is recommended that a person be employed to give a course in child training, so that the three phases of work for children — care, training, and feeding — may be represented in our teaching. The woman thus employed should give some time also to holding community clinics on child training in connection with the work of the home bureau agents.

Investigators should be employed to begin much-needed experimental work on foods and on economic conditions attending the purchase of food, shelter, and clothing.

The possibilities of securing funds for one or two additional buildings for the work in home economics should be given early consideration.

## METEOROLOGY

### W. M. Wilson, Professor of Meteorology

The Department of Meteorology has been seriously handicapped in its teaching work in the past year by the necessity of moving the laboratory in order to make room for other departments.

Meteorology was a required subject for the members of the Marine Corps and the Naval Cadets of the Student Army Training Corps. It was therefore necessary to have additional assistance for this work, which fortunately the College was able to supply. The regular university class work was carried on as usual. It is gratifying to note that the efforts of the Department have been recognized by the United States Commissioner of Education, who has placed this Department second on the list of institutions offering courses in meteorology and climatology.

The investigations started last year on (1) evaporation, (2) the effect of low temperatures on fruit buds, and (3) the climate of New York State and its relation to the agricultural industries of the State, are being continued.

## EXTENSION SERVICE

M. C. Burritt, Vice Director of Extension

In the following pages are given reports of the work of the Extension Service in (1) the Office of Administration, including resident teaching, extension schools, community meetings, farmers' institutes, fairs and exhibits, and the Cornell Reading Course for the Farm, (2) the Office of Publication, (3) the Office of the State Leader of County Agricultural Agents, and (4) the Office of the State Leader of Home Demonstration Agents.

### *Office of Administration*

The organization of county farm bureaus is now complete in all the agricultural counties of the State, and almost half of the counties have organized home bureaus for work with women. The policy during the year has been one of strengthening the organizations in the counties rather than seeking their expansion. This is particularly true of the home bureau associations, which have also been put on a membership basis. There are now more than 10,000 women affiliated with the twenty-five county associations and the two city groups. The county farm and home bureau associations are functioning as never before. The average membership is now about 1200 men and 400 women. The executive committees and the advisory committees have fully accepted the plan and are supporting it more actively than ever before. A beginning has been made in the development of the junior extnesion organization in the counties.

In order to foresee future extension needs, and if possible to evolve a well-balanced plan that will be within the probable resources of the State and the institution, each department of the College was asked to prepare a plan of work for the next ten years as its opportunities and needs now present themselves. The result of this was the presentation of a plan by each department, which is being taken as a basis for further study and discussion looking toward a definite and comprehensive enterprise.

More and more the plan of programs made jointly by the farm and home bureau organization, and by extension specialists or experts representing the scientific viewpoint of the College, is coming into use. As a result of annual conferences and of circular material and other means, each department in the College has now developed a fairly well-defined program. While each department is striving to round out its program

so as to consider all the factors in its field, naturally it has to take these factors one or two at a time and in order of importance. Thus, for example, the Department of Soil Technology is at present emphasizing the need of lime and drainage; Rural Engineering is dealing chiefly with drainage systems and tractors; and Farm Crops is stressing seed selection and improvement. These subjects by no means represent the entire fields in these departments, but they probably do represent fairly well the pressing problems. The programs of all the departments, as worked out in cooperation with the bureaus, constitute a state-wide program for the entire extension service.

This report would be incomplete if it did not point out again the pressing need of additional office space and a better arrangement of this space to the needs and organization of the Department. Between thirty-five and forty persons are working in fifteen small and very poorly arranged rooms. There is urgent need for from twenty to twenty-five offices, arranged with better relation one to another.

*Resident teaching.*— The teaching work of the Department was badly broken up in the first term of this year, many of the stronger men students being in military service. The second and third terms, however, showed a decided improvement. Winter-course registration in the Department was the lowest on record, there being only eight students in the extension course. The usual winter-course debate for the Morrison cup had to be abandoned as there were no departmental clubs. The contest for the extension prize in public speaking, however, was up to the average. Mrs. Florence M. Nevin, winner of the prize, presented a handsome silver cup to be retained by the College as a permanent prize, the names of the winners to be engraved on it each year.

For the second time, students in the regular extension courses were required to read that chapter of Dr. Andrew D. White's autobiography which relates to his ideas of education and the founding of Cornell University. They found it no task, and they all read much more than was required.

*Extension schools and community meetings.* — The number of extension schools held this year was about the same as for last year. An innovation this year was the three-days school, of which eight were held. One two-days school was also tried. These shorter schools presented only one phase of a farm problem. They were, for example, milking-machine schools, sheep-producers' schools, gas-engine schools, and the like. The three-days meeting seems very satisfactory and will be continued. The laboratory method has seen still further use in the past winter's schools, particularly in farm mechanics, which lends itself readily to actual partici-

pation, on the part of the farmers enrolled, in cleaning milking machines, overhauling and repairing gas engines, and similar operations. The record for the extension schools follows:

| | 1917–18 | 1918–19 |
|---|---|---|
| Number of schools held | 29 | 26 |
| Counties reached | 20 | 18 |
| Total enrollment | 993 | 794 |
| Average enrollment | 34.2 | 30.5 |
| Highest enrollment | 115 | 69 |
| Lowest enrollment | 15 | 7 |
| Average attendance per session | 17.4 | 20.2 |

On the other hand, the number of single-day or single-session community meetings in which college specialists participated as instructors was more than proportionately increased, and many requests from county agents and others for such assistance during the winter were declined because of our inability to take on any more work. Specialists in practically all departments carried a much heavier schedule than is desirable for the best interests of the work. One man carried a schedule of twenty consecutive weeks, averaging six days a week in the field or traveling, with only a single break of seven days at Christmas.

During the twelve-months period ending May 31, 1919, there were 2519 meetings held, with a total attendance of 130,077, or an average of 51.6 to each meeting; this may be compared with the figures for the same period a year ago, when 1472 meetings were held, with an attendance of 103,219, or an average of 70.1 to each meeting. During the month of March alone a total of 424 meetings were held, as compared with 381 meetings in March last year.

Roughly estimated, 75 per cent of these community meetings consist of series of from three to six consecutive days in one county. The programs of these meetings are closely related to the county agricultural program as worked out by the community committeemen in the farm bureau organization, and in this way serve to concentrate effort along definite lines having specific and more or less tangible results in view.

While a relatively large proportion of all meetings are still of a miscellaneous character — resulting, as they do, from requests coming mainly, either directly or indirectly, from granges, schools, farmers' clubs, and similar organizations, and therefore not being correlated with the county agricultural program which the farm bureaus are directing — a tremendous improvement has nevertheless been made over the condition of just a few years ago, when a very large part of our extension endeavor was almost necessarily miscellaneous.

*Farmers' institutes.*— By action of the State Legislature in 1918, the management of farmers' institutes and the appropriation for this work

were transferred from the State Department of Farms and Markets to this College. Here the work was attached to the Extension Service, under the same management as the extension schools and the community meetings. D. P. Witter, an experienced institute worker, was employed as farmers' institute adviser and has had immediate charge of the schedules and programs of institutes and the routing of workers.

The farmers' institutes were offered to the counties on the same financial terms as the other types of winter meetings, and with the understanding that the county agent should have a definite place on the program. Except on special request, the institutes were to consist of two sessions each instead of the former three sessions, and were not to include evening sessions. The assignment of institutes to counties on the basis of number of farms was discontinued; each county was allowed to have as many or as few institutes as the people wished. On the basis of this understanding, the communities asked for about 380 institutes, and 370 were actually scheduled. Twelve of these were subsequently canceled because of illness in the communities during the epidemic of influenza, leaving 358 meetings held, as compared with 338 in 1917–18.

The total attendance this year was 41,642 in 745 sessions, as compared with 50,777 last year in 902 sessions. The average attendance to a session this year was 56, the same as last year. The interest was reported good. The winter was mild, and this, combined with the very effective aid given by the county agents in the local transportation of speakers and equipment, gave the workers a very comfortable and satisfactory season. The following table shows the number of meetings and the attendance for this year and last:

| | 1917–18 | 1918–19 |
|---|---|---|
| Number of meetings | 338 | 358 |
| Number of sessions | 902 | 745 |
| Number of home-makers' conferences | 330 | 321 |
| Attendance | | |
| Total | 50,777 | 41,642 |
| Men | 39,937 | 33,160 |
| Women | 10,840 | 8,482 |
| Average attendance per session | 56 | 56 |
| Women | ..... | 26 |

*Fairs and exhibits.*— During the season of 1918 the College of Agriculture was called upon to send exhibits to the State Fair, the Rochester Industrial Exposition, 46 county fairs, the meeting of the New York State Horticultural Society, and the National Milk and Dairy Farm Exposition. At the State Fair, the College was allowed the use of part of its former space in the State Institutional Building. The exhibits returned to the usual type, with emphasis placed on subjects of special

importance in production and conservation of crops. In addition to the regular exhibits, the College cooperated with the New York State Food Commission in an exhibit of wool and an exhibit and demonstration on tractors, ditching machines, and concrete-tile making. Cooperation was maintained also with the State Department of Farms and Markets, through the Department of Dairy Industry of the College, by an exhibit and demonstration in making cheese, butter, and ice cream, held in the Dairy Building. Ten departments from the College contributed to these exhibits. The Department of Animal Husbandry staged an exhibit on the cost of raising a cow, showing the feed required in raising the animal to maturity and the cost of keeping the mature cow for one year, together with the product returned. The Departments of Rural Engineering and Soil Technology combined in putting up an exhibit on drainage, showing especially models of types of outlets, the method of leveling, the laying out of a drainage system, and a model power ditching machine in operation. In addition to this exhibit in the State Institutional Building, tractor and demonstration exhibits were maintained on the fair ground each day. The making of concrete tile was also demonstrated in connection with the ditching demonstration. The Department of Farm Crops arranged an exhibit laying special emphasis on home-grown seeds. The Department of Poultry Husbandry emphasized in its exhibit the importance of selection. The Departments of Plant Breeding, Plant Pathology, and Entomology cooperated in preparing a bean exhibit which showed particularly the results obtained in the experimental laboratory at Perry, New York. Also, the Departments of Plant Pathology and Entomology cooperated with the New York State Experiment Station at Geneva in placing a pathological and entomological exhibit in the Fruit Building. The Department of Floriculture arranged an exhibit in connection with the flower show. The junior extension work was shown by an exhibit placed in connection with the boys' and girls' department.

Two departments from the College contributed to the exhibits sent to the Rochester Exposition. These were the Departments of Plant Pathology and Entomology. A combined exhibit was arranged, treating especially of fruit diseases and insects. The same departments cooperated in staging exhibits at the meeting of the New York State Horticultural Society.

At the county fairs, the College cooperated with the New York State Food Commission and the county farm bureaus. The College prepared the exhibits and furnished the representative to accompany and explain them, the local farm bureau made the arrangements with the fair association, and the New York State Food Commission paid the transportation charges on the exhibits and the expenses of the expert in charge. There

were seven exhibits furnished by the College, and these were sent to forty-six county fairs. In these exhibits special emphasis was laid on the subjects being pushed by the Food Commission, and all had to do with food production and conservation. There was an exhibit relating to the sheep industry which emphasized the important factors involved in raising sheep, particularly in the production and marketing of wool. Exhibits on plant diseases and insect pests were also prepared, showing the economic importance of these pests and diseases, and methods of prevention. The Department of Farm Crops made a special drive on home-grown feeds, with emphasis laid on the growing and the feeding value of legumes. The poultry exhibits were prepared to show ways and means for selecting hens for egg production and breeding purposes. This was a part of the regular campaign on selection which was waged in every county. The drainage exhibit held at the State Fair by the Department of Rural Engineering was sent also to several county fairs, and in addition to these departmental exhibits the state labor specialist assembled an exhibit of labor-saving devices.

The distribution of exhibits, the approximate number of consultations, and the probable number of persons who saw the exhibits, may be summarized as follows: exhibits were sent to 37 counties; 7 of these counties had two exhibits, and 1 county had three; every county that asked for an exhibit received one; approximately 60,725 persons saw the exhibits, and consultations were held by the specialists with 3864 persons; extension specialists from seven departments spent 185 days at the county fairs, not including time spent in traveling.

In April of 1919, a second National Milk and Dairy Farm Exposition was held in New York City. As in the previous year, the College cooperated with the State Department of Farms and Markets in preparing several exhibits. The exhibits with which the College was particularly concerned related to the cost of milk production, the care and testing of milk and of milk products, the manufacturing of cheese, butter, and ice cream, the food value of milk, and the making of milk and its products into many articles of diet. The cost of milk production was shown graphically by a large chart in the rear of the exhibit, on which the factors entering into the cost of producing milk were listed and the actual material needed to produce 100 pounds of milk was indicated. Labor was represented by a farm family from Orange County consisting of the owner and his wife, his son, and a hired man. The testing of milk and butter and the plating of milk for bacteria count was demonstrated every hour. Much interest was centered in the manufacture of butter, cheese, and ice cream. This was all sold in small sample lots to demonstrate the value of pure-milk products. The food value of milk and its use in many

articles of diet was made plain to the visitor by demonstrations in making these dishes and by the opportunity given to sample the food so prepared. Recipes for making these several dishes were given on request. As a definite experiment on the food value of milk, two calves were shown, one of which had been fed whole milk since birth and the other had been fed the best milk substitutes after having been well started on whole milk. After five weeks the result was striking; the milk-fed calf had gained weight, while the other had lost.

*Farmers' Week.*— The twelfth annual Farmers' Week, held at the College February 10 to 14, 1919, was marked by a larger attendance than any other Farmers' Week since the beginning of this annual event. There were a large number of women present, 1508 being registered. The total registration, 3763 persons, represented attendance from every agricultural county in the State, and, in addition to those registered from New York State, persons were registered from twenty-two other States, from Canada, and from Washington, D. C.

The program consisted of 237 lectures, 80 demonstrations, and 85 conferences and discussion periods. The most emphasis was placed on the demonstrations and the conference groups. Four state associations held their meetings in connection with Farmers' Week, as well as several specialized associations working in close conjunction with the College.

*Cornell Reading Course for the Farm.*— At the close of the year 1918–19 the Reading Course for the Farm will have completed eight years lacking three months. During this time ninety lessons have been issued and the enrollment has grown rapidly. The following figures indicate the enrollment after the annual revision of the mailing list:

| | |
|---|---|
| 1911–12 | 2,310 |
| 1912–13 | 3,884 |
| 1913–14 | 5,877 |
| 1914–15 | 12,984 |
| 1915–16 | 20,560 |
| 1916–17 | 22,739 |
| 1917–18 | 31,032 |
| 1918–19 | 37,477 |

The enrollment for this year includes 26,414 readers continued from the previous year, 2024 old readers renewed, and 9039 new readers.

The Reading Course has had close relationship with the farm bureaus, having sent 190 publication charts and 57 classified sets of extension publications to the county agents. These charts have been displayed at farmers' institutes, fairs, and community meetings, and in farm bureau offices. County agents have sent to the reading-course office lists of farm-bureau members to be added to the mailing list, and have procured

supplies of the lessons for distribution. The names from twenty-five counties have been placed on a temporary mailing list to be revised this summer.

The high-school teachers of agriculture this year used 6020 reading-course lessons in classroom instruction and for distribution. Thirteen high-school teachers have obtained classified sets of extension publications for reference use.

Cooperation with the State Grange has been undertaken during the past year by preparing with the Department of Home Economics eleven suggested outlines for use by grange lecturers. One thousand copies of these outlines have been distributed by the state lecturer at lecturers' conferences. The outlines are based on reading-course lessons which are to provide subject matter for discussion. A short history of the National Grange was prepared.

Publication charts have been prepared for conductors of farmers' institutes and extension schools, and an effort has been made to get enrollments in the reading courses at these meetings. Over 1200 registrations have been obtained at institutes during the past year. At Farmers' Week 2037 enrollments were made in the reading courses.

An interest in correspondence courses has been manifested in the last few years, which has made itself felt in the College of Agriculture. The reading-course office has endeavored to meet the demand by organizing three advanced reading courses, in farm crops, vegetable gardening, and fruit growing, respectively. During the year 112 advanced readers submitted 462 reports.

Eleven study clubs in agriculture, of which seven are new clubs and four are old ones renewed, have been conducted in local communities. One of these is located at a state hospital and its members are officials engaged in agricultural work. If similar study clubs can be organized at other state institutions, they may contribute to the successful management of the farms operated by the State.

Over 165,000 lessons were distributed otherwise than to the mailing list during the year. The number of lessons sent out on individual request was over 95,000. The number of requests received and the number of lessons asked for were greater in each case than for any previous year. The value of the service rendered by some of the reading-course lessons is illustrated by the fact that a milk company asked permission to reprint at its expense 10,000 copies of lesson 135, *The Farm Ice Supply*, for distribution to its patrons, and a local condensery used 800 copies of the same lesson for personal distribution. The special distribution of reading-course lessons during the past year, aside from those sent to the mailing list, is indicated in the following table:

| | Number of copies sent |
|---|---|
| Sent in reply to 20,652 requests through the mail (including discussion papers) | 95,429 |
| Distributed at 372 farmers' institutes (selected by programs) | 51,525 |
| Classified sets as samples (39 classified sets, 101 publications in each) | 3,939 |
| Charts (121 charts displaying 16 publications each) | 1,936 |
| Exhibits (milk exposition, special demonstration car) | 5,000 (est.) |
| For classroom use and to visitors | 8,000 (est.) |
| Total yearly distribution other than to mailing list | 165,829 |

*Office of Publication*

During the year ending June 30, 1919, the three outstanding features of the work of the Office of Publication concerned each of the three main branches of its work — editorial revision, distribution of publications, and extension through print in newspapers and periodicals.

The distribution of publications is on a far better basis than heretofore, due to careful organization and supervision of the work under M. V. Atwood, who has devoted untiring effort to the improvement of the methods used. More work has been done than in any preceding year, and accumulated supplies of many publications have been advantageously distributed. A large part of this work had to do with emergency bulletins connected with food production and food conservation.

The information service to the press of the State achieved better results this year than ever before, and only those clippings that were actually received from matter furnished by the College to the papers showed a circulation of 67,236,205 separate printings. The cooperation between the College and the editors of the State has grown closer and more effective, until now the information service of the College is the basis of a large part of the farm and home news carried by the daily and the weekly press. The Office is now building up an actual extension service to the rural press and this is being well received.

On July 1, 1918, the Office was given the additional duty of editing and issuing the *Extension Service News*, a monthly organ for the development of a state-wide understanding of extension in agriculture and home economics by those who are connected with the work at the College and in the farm and home bureaus.

From July 1 to October 1, Professor Adams devoted his vacation period to the work of the Federal Department of Agriculture in the war campaign for the stimulation of food production, and from October 1 until after the signing of the armistice on November 11 he was in service with the Military Intelligence Division of the General Staff, U. S. A., at Washington.

The end of the year finds the work of the Office in better shape than it has ever been heretofore. The greatest drawback to future development is the lack of suitable space for storage and workrooms in connection with the distribution of publications. The Office is also in need of an additional assistant editor, part of whose duties would be to help develop a special news service to the strictly agricultural and home-making publications. The College has a much larger quantity of useful information, which is constantly in demand, than it can furnish through the present channels of a limited editorial and administrative force.

*Office of the State Leader of County Agricultural Agents*

The important outstanding features of the county agent work in New York State during the past year are: (1) the completion and strengthening of the farm bureau organization in every county and rural community; (2) the development of state-wide uniformity along definite and permanent lines in the several projects covering demonstration work; and (3) the handling of emergency work required by the exigencies of the reconstruction period.

The close of the year finds a well-organized farm bureau association in each of the 55 agricultural counties in New York State. The remaining seven counties are either urban (Bronx, Kings, New York, Queens, and Richmond) or forestal (Hamilton and Putnam). Since July 1, 1918, Lewis County, the last of the so-called agricultural counties in the State, definitely organized the Lewis County Farm Bureau Association. This county had previously been operating under a temporary arrangement. The organization was perfected in December, 1918.

As the county agent work develops in this State, it becomes more and more evident that stability and permanent progress in the work is dependent on a large representative farmer membership, together with the encouragement for initiative of expression and action from the farmers living within the two thousand and odd communities in the State. It is evident also that such initiative is being taken by the farmers. Reference to the following table will emphasize this point more clearly:

| County | Paid members July 1, 1918 | Paid members June 30, 1919 | Percentage of farmers who are members |
|---|---|---|---|
| Albany | 721 | 1,258 | 39.9 |
| Allegany | 498 | 1,030 | 20.8 |
| Broome | 725 | 1,150 | 28.6 |
| Cattaraugus | 1,252 | 1,800 | 29.9 |
| Cayuga | 1,152 | 2,171 | 45.3 |

| County | Paid members July 1, 1918 | Paid members June 30, 1919 | Percentage of farmers who are members |
|---|---|---|---|
| Chautauqua | 1,000 | 1,548 | 20.6 |
| Chemung | 609 | 886 | 40.4 |
| Chenango | 1,025 | 1,300 | 30.5 |
| Clinton | 253 | 681 | 18.8 |
| Columbia | 758 | 1,074 | 36.2 |
| Cortland | 825 | 1,020 | 39.0 |
| Delaware | 1,215 | 1,716 | 34.0 |
| Dutchess | 510 | 800 | 22.2 |
| Erie | 1,004 | 1,936 | 23.6 |
| Essex | 213 | 755 | 33.1 |
| Franklin | 908 | 985 | 26.8 |
| Fulton | 245 | 439 | 22.7 |
| Genesee | 1,016 | 1,674 | 51.4 |
| Greene | 376 | 535 | 20.1 |
| Herkimer | 1,437 | 1,700 | 54.9 |
| Jefferson | 1,030 | 1,250 | 21.6 |
| Lewis | 256 | 557 | 16.6 |
| Livingston | 938 | 1,370 | 41.5 |
| Madison | 902 | 2,105 | 52.9 |
| Monroe | 1,430 | 1,959 | 32.8 |
| Montgomery | 587 | 885 | 40.4 |
| Nassau | 482 | 671 | 65.9 |
| Niagara | 1,335 | 2,294 | 52.8 |
| Oneida | 705 | 1,607 | 23.1 |
| Onondaga | 770 | 1,275 | 22.0 |
| Ontario | 675 | 1,194 | 27.0 |
| Orange | 1,812 | 1,964 | 49.9 |
| Orleans | 1,020 | 1,520 | 54.6 |
| Oswego | 640 | 850 | 13.4 |
| Otsego | 1,872 | 2,283 | 42.7 |
| Rensselaer | 497 | 724 | 19.8 |
| Rockland | 230 | 251 | 22.1 |
| St. Lawrence | 636 | 1,281 | 14.3 |
| Saratoga | 317 | 579 | 16.0 |
| Schenectady | 283 | 486 | 47.3 |
| Schoharie | 945 | 1,591 | 48.3 |
| Schuyler | 520 | 627 | 32.7 |
| Seneca | 627 | 857 | 41.1 |
| Steuben | 976 | 1,896 | 25.7 |
| Suffolk | 576 | 944 | 37.8 |
| Sullivan | 454 | 575 | 14.4 |
| Tioga | 1,267 | 1,974 | 69.0 |
| Tompkins | 1,063 | 1,352 | 45.3 |
| Ulster | 595 | 672 | 13.3 |
| Warren | 377 | 459 | 24.6 |
| Washington | 517 | 1,032 | 28.9 |
| Wayne | 1,493 | 2,207 | 41.9 |
| Westchester | 276 | 455 | 24.2 |
| Wyoming | 1,143 | 1,505 | 39.8 |
| Yates | 624 | 1,026 | 45.3 |
| Total | 43,612 | 66,735 | ..... |
| Average | 793 | 1,213 | 31.3 |

On July 1, 1918, the average farm bureau membership was 793 per county, and on June 30, 1919, it was 1213 per county. The total number of farm bureau memberships recorded for the year ending June 30, 1918, was 43,612. One year later, June 30, 1919, the membership had increased to 66,735, this being 31.3 per cent of the farms in the State. This remarkable growth clearly illustrates the fact that the farm bureaus are performing a service and that this service is being appreciated by the farmers.

For the past several years the membership campaigns have been carried out over the greater part of the year. This has been unsatisfactory in several respects, chiefly in the burden it has placed on the committeemen. Practically all of the campaigns conducted for this year were held between November 25, 1918, and January 1, 1919, thus definitely completing this part of the program of the bureaus for the year. By systematically organizing and conducting these campaigns the task is performed with much greater satisfaction.

A more or less definitely outlined agricultural community still seems to be the logical unit of territory within which to perfect farm bureau organization and to conduct various lines of demonstration work. A school district is now conceded by most of the farm bureau associations to provide for the most equitable distribution of territory to be represented by each committeeman. The school district is a well-known area, and a committeeman is designated to represent each school district. In every agricultural community there are from three to five or more school districts. This delineation of territory to be represented by each committeeman is particularly advantageous in membership campaigns.

The activities of the central office force for the year were as follows:

| | |
|---|---|
| Days in office | 621 |
| Days in field | 583½ |
| Days on leave | 56 |
| Total number of counties visited | 464 |
| Number of conferences with agents | 363 |
| Number of executive committees met | 195 |
| Attendance at these meetings | 923 |
| Number of other county committee meetings attended | 134 |
| Attendance at these meetings | 10,910 |
| Number of all other meetings addressed | 25 |
| Attendance at these meetings | 1,196 |
| Number of letters written | 4,863 |
| Miles traveled by rail | 67,160 |
| Miles traveled by other means | 7,076⅔ |
| Total expense of travel | $3,981.95 |
| Number of circular letters to agents | 79 |
| Circulation | 5,000 |
| Number of circular letters to farm bureau association presidents | 7 |
| Circulation | 805 |

The annual conference of county agricultural agents and extension specialists was held at the College of Agriculture from October 28 to November 2, 1918. For the first time the programs of the annual county-agent conference and the Normal Institute were combined. With one exception the program followed was similar to that in former years, the exception being that a laboratory method was used to convey desired information to the county agents. The advantage of this plan is that the subject concerned is presented before a small body of county agents, thus giving more time for personal discussion. Each laboratory leader presented his subject matter four times in four successive periods during the afternoon. These laboratory periods proved to be very successful and a number of requests were registered for the continuation of this plan at the next conference.

There has been a decided inclination toward a state-wide program along definite and uniform lines for conducting field demonstration work. A community program, based on the needs of the community as expressed by the farmers, has been frequently emphasized. It is important that so far as practicable community programs should be shaped so that they may become integral parts of the county and state programs. Up to the present time, however, no clearly definite state program has been formulated. Now that the entire State is organizing, and county programs of work are being approved by the county advisory committees, it is possible that a state program may be evolved. Any such program will of necessity be general in nature.

Working in close harmony with the regularly organized home departments and the emergency home demonstration agents, the county agents have rendered services to the women of the State. This work is covered more fully in the report of the state leader of home demonstration work. There is a growing recognition of the fact that the home work should be on a par with farm work, and a definite movement to create joint farm-and-home-bureau executive committees with constitutions and by-laws to govern them. At the end of the year 1918–19, twenty-five county bureaus are signifying their intention to change their present form of organization to provide for a joint farm-and-home-bureau organization.

With the end of the fiscal year the war emergency funds provided to stimulate agricultural production were withdrawn. The direct result of this curtailment as affecting farm bureau work has been the dropping of many assistant county agents, for the reason that the county associations had not sufficient funds to pay the salaries of assistants. As an indirect result of this, a slight decrease in the amount of field work may

be expected during the ensuing year. On the other hand, it has been gratifying to note that the withdrawal of these funds has, in some instances at least, served to stimulate the county associations to greater appreciation of the importance of self-reliance. In all probability the farmers will more and more take upon themselves the responsibility for raising the needed funds to adequately maintain the bureaus. We may expect to see the farm bureau membership fee increased above the customary one dollar a year, and other local sources of support may also be developed.

*Office of the State Leader of Home Demonstration Agents*

At the beginning of the year 1918–19 there were 33 counties in which home demonstration agents were working. In 5 of these counties the work was permanently organized as home economics departments of the farm bureau, while in the remaining 28 counties the work was conducted as a war measure with very little organization. The reports show that the home demonstration agents and the county committees concentrated their efforts on demonstrations of sugar saving and wheat saving during the summer of 1918. Because they met a great need, community kitchens were organized; the value of pressure canners as an economical piece of equipment in food conservation, fuel conservation, and time conservation was emphasized; and exhibits at fairs were made.

Many sugar-saving demonstrations were given during the summer. There was a great demand for this work, because of the practical problems which housekeepers were meeting in planning meals and canning with the small amount of sugar available, and the necessity of using various kinds of sugar. There was a great demand also for demonstrations of wheat-saving breads and cakes. The home demonstration agents experimented with recipes that came from the College and from other sources, to determine which were best adapted for use in each county because of the grains available in that locality. They both demonstrated and exhibited the results which they believed to be satisfactory.

As a result of the shortage of food caused by the war emergency, and the necessity of canning and of preventing waste, much interest was aroused for the organization of centers where housekeepers could get together for the purpose of meeting the situation. This led to the development of community kitchens, which were provided with the most up-to-date equipment. During the summer of 1918, a total of 55 kitchens were established in twenty-five counties through the cooperation of the county agents with the local committees. In many places the community kitchen had a wider scope of work than the preservation of food alone. Many of the kitchens served as information and demonstration centers. Each

kitchen was under the supervision of the home demonstration agent, with a paid manager or the community committee directly in charge. Excellent cooperation was secured in this work, resulting in the development of a community spirit which has outlived the war.

The distribution of kitchens by counties, and the amount of material preserved, are as follows:

| County | Number of kitchens | Total number of jars of vegetables and fruits | Total number of jars of jams and jellies | Total number of pounds of dried products |
|---|---|---|---|---|
| Broome | 1 | No report | ..... | ..... |
| Cayuga | 1 | No report | ..... | ..... |
| Chautauqua | 4 | 1,895 | ..... | 25 |
| Cortland | 1 | Diet kitchen | ..... | ..... |
| Delaware | 2 | No report | ..... | ..... |
| Fulton | 2 | 7,188 | 3,208 | 78 |
| Herkimer | 2 | No report | ..... | ..... |
| Jefferson | 1 | Diet kitchen | ..... | ..... |
| Monroe | 3 | 1,558 | 89 | ..... |
| Montgomery | 1 | 750 | ..... | ..... |
| Nassau | 7 | 24,890 | 1,585 | 5,338 |
| Niagara | 1 | No report | ..... | ..... |
| Oneida | 3 | 4,770 (est.) | ..... | ..... |
| Onondaga | 4 | 14,395 | 418 | 290 |
| Ontario | 2 | 1,800 | ..... | ..... |
| Otsego | 2 | 7,477 | ..... | 245 |
| Rensselaer | 1 | No report | ..... | ..... |
| Rockland | 1 | 770 | 800 | ..... |
| Saratoga | 1 | 3,169 | 624 | ..... |
| Steuben | 1 | 2,244 | ..... | 72 |
| Tioga | 1 | 3,027 | 150 | ..... |
| Tompkins | 2 | 5,983 | 270 | ..... |
| Ulster | 2 | 2,800 | 240 | ..... |
| Wayne | 2 | 3,039 | ..... | ..... |
| Westchester | 7 | 15,645 | 2,040 | 29,730 |
| Total | 55 | 101,400 | 9,424 | 35,778 |

In addition to the counties tabulated, the transfer of the work of the New York State Food Commission in Buffalo and Syracuse to the State Extension Service has added three community thrift kitchens since February 1. The Buffalo thrift kitchen developed, as its leading feature, an ambitious project in the dehydrating of fruits and vegetables. A second thrift kitchen was established in a foreign section of Buffalo. In Syracuse the thrift kitchen not only served as a means for the cooperative preservation of food, but also became a center for information regarding better housekeeping. For example, between February 1 and June 1 the kitchen received requests for assistance from 448 callers, 759 persons who tele-

phoned, and 302 persons who sent letters; in addition to these, 3469 persons attended demonstrations at the kitchen.

As a means of preserving food with the use of a minimum amount of time, labor, and fuel, the value of pressure canners was demonstrated by the agents. As a result of the demonstrations, 49 pressure canners were officially purchased by 22 county committees, and this was followed by the purchase of many others by communities and individuals. In one county 78 pressure canners were bought through the home bureau. The women of the communities purchasing these canners were so well satisfied with the results that more are being bought all the time through the home bureau at a saving of 20 per cent on each canner.

The summer and early fall months are the times when the agents receive many requests for exhibits and demonstrations at fairs. Because of the many unusual problems that the women were meeting in the early part of this year, due to war conditions, a special effort was made to provide helpful and suggestive means of meeting these problems. As many as five hundred women were reached personally through exhibits at a single fair of from three to five days. The exhibits included displays of sugar-saving foods, labor-saving devices, and home conveniences. Bulletins and pamphlets were also distributed by agents and committeemen to women who were particularly interested and wanted some specific help. This enabled the agent to meet personally large numbers of county women and to learn more of the community and individual problems. It also helped develop a point of contact for future home calls.

Since this is a time when great results are proceeding from organization, it was decided not to continue the work after December in any county where there was not sufficient interest to support the work in an organized way. Accordingly a policy was determined upon whereby federal or state funds would not be paid toward the salary of a home demonstration agent unless the county met two requirements: (1) support and interest evidenced by at least 300 women joining the association; (2) an appropriation and membership fees totaling at least $1500. In order to meet these requirements the executive committees and the home demonstration agents concentrated their efforts during the fall on community organization as a background for membership campaigns. As a result, 25 of the 33 counties received appropriations and secured memberships which warranted the continuation of the work.

Community organization also progresses at the present time. The reports show a total of 651 organized communities with 2027 committeemen.

Following is a list of the counties receiving appropriations and the paid membership to date:

| County or city | Appropriation | Paid membership |
|---|---|---|
| **County** | | |
| Allegany | $1,500 | 403 |
| Broome | 1,200 | 320 |
| Cayuga | 1,200 | 428 |
| Chenango | 1,200 | 400 |
| Cortland | 750 | 400 |
| Delaware | 300 (½ year) | 205 |
| Erie | 3,100 | 200 |
| Jefferson | 1,500 | 719 |
| Monroe | 1,300 | 330 |
| Nassau | 3,745 | 400 |
| Niagara | 1,500 | 188 |
| Oneida | 2,809 | 547 |
| Onondaga | 1,000 | 350 |
| Orleans | 1,000 | 303 |
| Oswego | 1,000 | 645 |
| Otsego | 1,600 | 1,104 |
| Rensselaer | 1,000 | 302 |
| Saratoga | 1,200 | 276 |
| Steuben | 1,000 | 257 |
| Suffolk | 1,000 | 165 |
| Sullivan | 750 | 203 |
| Tioga | 1,000 | 427 |
| Ulster | ..... | 383 |
| Wayne | 750 | 373 |
| Westchester | 1,500 | 647 |
| **City** | | |
| Buffalo | 500 (2 months) | 450 |
| Syracuse | 1,500 (½ year) | 430 |

During the winter and spring, projects were adopted by the communities. Since the organization was perfected with a certainty that the work would continue, it became possible to make more definite plans for a definite piece of work. During these months the greatest interest was evidenced in nutrition, health, foods, clothing, civics, school lunches, and cooperative projects.

One step measuring progress in the development of the home bureau organization was the realization by the agents that they could not be responsible for all the work in the county and that the number of projects would have to be limited unless leaders could be found. With this realization, community leaders were sought who were experts in the various projects and were willing to accept the responsibility in their own community. This has been the means of multiplying many times the effect of the work of the home demonstration agent.

In order to give the local leaders suggestions and help for their work, as well as to make it possible to adhere to uniformity of work, training

schools have been held for local leaders. During the summer of 1918, fifteen of these schools were held in food preservation alone, and were attended by 417 persons. Since that time training schools have been held for the training of local leaders in clothing, health, and thrift. In several counties, local leaders are directly responsible for all junior work. Agents and executive committees are looking forward to broadening the service and increasing the support of home bureaus by discovering, training, and utilizing more of such workers in the future.

Women are recognized as being the users of money for the household, and it is interesting to note that already the home bureau organization is helping the housewife in this respect. Through the home bureau many cooperative projects have been started, and women are buying, through the bureau, pressure canners, magazines, soapstones for fireless cookers, cans, can rubbers, dyes, books, seeds, and dress forms. The desire to cooperate for the benefit of others has also led to the organization of community rest rooms, a women's exchange, community centers, community kitchens, a cafeteria, and sewing rooms. The possibilities along these lines are boundless.

That the home bureau organization is becoming a force in the counties is demonstrated by the numerous calls for cooperation from various organizations in the counties. It is recognized that there are many women's organizations conducting similar types of work, in fact overlapping, and that it is only by cooperation that all can function at their maximum. The reports from agents show that they are cooperating with the Grange, the Red Cross, social workers, schools, boards of education, Camp-Fire Girls, women's clubs, the Women's Christian Temperance Union, the Dairymen's League, the Young Women's Christian Association, county poor farms, associated charities, community nurses, churches, library associations, and mothers' clubs.

Steps are now being taken for the organization of a federation of home bureaus. At a meeting held in Ithaca in Farmers' Week of 1919, which was attended by 80 women representing about 27 home bureaus in New York State, a committee for the organizing of such a federation was elected. This committee has already had one meeting and is planning for another at an early date. The women feel that the work can be greatly strengthened by such a federation, which will make it possible for each county to know more of the successes or failures in other counties. The contemplation of such an organization marks progress.

The first step taken to link more closely the farm and home departments was through joint executive meetings of the two departments. This has brought about more sympathetic and cordial relationships through

an understanding of the work and the plans of each department. A meeting has been held in practically every county, and two meetings have been held in several counties.

The following summary indicates the work accomplished during the fiscal year:

| | |
|---|---|
| Days in office | 3,325½ |
| Days in field | 3,996 |
| Days in laboratory | 288½ |
| Number of meetings held | 2,866 |
| Attendance at meetings | 139,283 |
| Number of demonstrations held | 1,082 |
| Attendance at demonstrations | 46,621 |
| Number of personal letters written | 23,291 |
| Number of circular letters sent | 89,092 |
| Number of calls received at office | 8,134 |
| Number of calls made at homes | 5,373 |
| Number of press notices sent out | 4,266 |

## FINANCIAL REPORT OF THE NEW YORK STATE COLLEGE OF AGRICULTURE JULY 1, 1918, TO JUNE 30, 1919

### Income from Students

| | | |
|---|---|---|
| Tuition, Regular | $30,117.50 | |
| Winter courses | 375.00 | |
| Summer school | 2,161.30 | |
| Student fines | 544.00 | $33,197.80 |
| Laboratory fees: | | |
| Dairy Industry | $1,315.75 | |
| Poultry Husbandry | 103.00 | |
| Entomology | 1,499.50 | |
| Farm Crops | 429.50 | |
| Botany | 2,109.79 | |
| Floriculture | 380.50 | |
| Forestry | 50.00 | |
| Landscape Art | 53.50 | |
| Plant Breeding | 47.50 | |
| Plant Pathology | 637.03 | |
| Pomology | 285.00 | |
| Farm Management | 144.50 | |
| Home Economics | 6,006.75 | |
| Rural Education | 6.00 | |
| Meteorology | 228.54 | |
| Rural Engineering | 390.00 | |
| Soil Technology | 227.70 | 13,914.56 |
| Total | | $47,112.36 |

### Income from Sales and Services

| | |
|---|---|
| Administration: | |
| General | $ 3,236.98 |
| Business Office | 46.43 |
| Publication Office | 671.94 |
| Library | 450.00 |
| Engineer's Office | 1,904.92 |
| Grounds | 150.35 |
| Lockers | 69.75 |
| Animal Husbandry | 16,148.12 |
| Dairy Industry | 28,651.72 |
| Poultry Husbandry | 9,671.31 |
| Entomology | 988.13 |
| Farm Crops | 1,603.86 |
| Farm Practice | 17,935.72 |
| Botany | 1,843.01 |
| Floriculture | 2,380.26 |
| Forestry | 643.41 |
| Landscape Art | 69.60 |

| | |
|---|---|
| Plant Breeding | $ 198.01 |
| Plant Pathology | 317.89 |
| Pomology | 1,582.08 |
| Farm Bureau | 13.28 |
| Farm Management | 22.26 |
| Home Economics | 46,322.18 |
| Rural Economy | 103.33 |
| Rural Education | 121.62 |
| Rural Engineering | 701.92 |
| Soil Technology | 403.38 |
| Extension Department | 7,998.76 |
| Mess Hall | 45,257.10 |
| Total | $189,507.32 |

**Expenditures — State and Income Funds**

(Exclusive of transfers between departments)

| | | |
|---|---|---|
| Salaries for instruction, research, and extension work | | $483,127.12 |
| Administrative and general: | | |
| Administrative salaries | $71,213.50 | |
| General administrative expense | 42,911.01 | |
| Dean's Office | 753.58 | |
| Secretary's Office | 2,062.29 | |
| Business Office | 2,312.45 | |
| Publication Office | 8,738.55 | |
| Library | 3,059.05 | |
| Engineer's Office | 12,926.20 | |
| Grounds | 5,155.17 | |
| Fuel, light, power, and water | 54,775.83 | |
| Lockers | 32.50 | |
| Repairs | 9,443.37 | $213,383.50 |
| Departmental: | | |
| Animal Husbandry | $45,165.77 | |
| Poultry Husbandry | 14,396.14 | |
| Dairy Industry | 17,575.66 | |
| Entomology | 5,719.13 | |
| Farm Crops | 5,946.06 | |
| Farm Practice | 28,611.66 | |
| Botany | 5,254.69 | |
| Floriculture | 3,292.13 | |
| Forestry | 2,020.00 | |
| Landscape Art | 1,589.79 | |
| Plant Breeding | 2,729.84 | |
| Plant Pathology | 5,593.12 | |
| Pomology | 4,683.67 | |
| Farm Management | 2,509.84 | |
| Farm Bureau | 1,092.34 | |

| | | |
|---|---|---|
| Departmental (*continued*): | | |
| Home Economics | $52,189.61 | |
| Rural Economy | 1,858.60 | |
| Rural Education | 3,034.42 | |
| Rural Organization | 1,348.04 | |
| Agricultural Chemistry | 1,603.35 | |
| Drawing | 227.91 | |
| Meteorology | 322.25 | |
| Rural Engineering | 3,124.46 | |
| Soil Technology | 3,203.75 | |
| Extension Department | 41,328.40 | |
| Summer school | 2,000.97 | |
| Investigation of bean production | 1,547.90 | |
| Game Farm | 5,660.62 | |
| Mess Hall | 45,257.10 | |
| Smith-Hughes work | 11,510.31 | $320,397.53 |
| Total | | $1,016,908.15 |

**State Maintenance Appropriation, 1917–18**

| | | |
|---|---|---|
| Appropriation | | $709,651.00 |
| Expenditures previously reported | | 638,444.37 |
| Balance unexpended July 1, 1918 | | $71,206.63 |
| Expenditures subsequent to July 1, 1918, on liabilities incurred prior to that date: | | |
| Administration: | | |
| General | $1,043.16 | |
| Dean's Office | 20.10 | |
| Secretary's Office | 109.00 | |
| Business Office | 65.15 | |
| Publication Office | 709.73 | |
| Engineer's Office | 103.16 | |
| Grounds | 72.00 | |
| Fuel, light, power, and water | 1,546.53 | |
| Animal Husbandry | 999.75 | |
| Dairy Industry | 187.40 | |
| Entomology | 108.50 | |
| Farm Crops | 50.02 | |
| Farm Practice | 47.05 | |
| Botany | 487.98 | |
| Floriculture | 18.09 | |
| Forestry | 278.18 | |
| Landscape Art | 178.02 | |
| Plant Breeding | 30.76 | |
| Plant Pathology | 267.49 | |
| Pomology | 302.29 | |
| Vegetable Gardening | 98.04 | |
| Farm Management | 127.58 | |

| | | |
|---|---|---|
| Home Economics | $ 66.71 | |
| Rural Economy | 36.08 | |
| Rural Education | 16.52 | |
| Agricultural Chemistry | 190.65 | |
| Drawing | 27.65 | |
| Rural Engineering | 208.37 | |
| Soil Technology | 142.45 | |
| Extension Department | 720.23 | |
| Repairs | 2,638.88 | |
| Salaries | 723.18 | $11,620.70 |
| Balance of appropriation lapsed | | $59,585.93 |

**State Maintenance Appropriation, 1918–19**

| | | |
|---|---|---|
| Appropriation | | $874,738.00 |
| Expenditures: | | |
| Administration: | | |
| General | $ 34,696.80 | |
| Dean's Office | 733.48 | |
| Secretary's Office | 1,830.86 | |
| Business Office | 1,871.06 | |
| Publication Office | 6,912.70 | |
| Library | 2,518.62 | |
| Engineer's Office | 7,394.28 | |
| Grounds | 3,842.95 | |
| Fuel, light, power, and water | 44,592.06 | |
| Animal Husbandry | 15,480.21 | |
| Poultry Husbandry | 4,666.42 | |
| Dairy Industry | 5,399.75 | |
| Entomology | 3,579.31 | |
| Farm Crops | 4,152.51 | |
| Farm Practice | 3,423.30 | |
| Botany | 1,544.34 | |
| Floriculture | 1,271.80 | |
| Forestry | 1,440.50 | |
| Landscape Art | 1,392.82 | |
| Plant Breeding | 1,847.60 | |
| Plant Pathology | 3,815.33 | |
| Pomology | 3,579.86 | |
| Farm Management | 2,156.57 | |
| Farm Bureau | 1,012.30 | |
| Home Economics | 4,778.84 | |
| Rural Economy | 1,497.27 | |
| Rural Education | 2,902.20 | |
| Rural Organization | 1,325.32 | |
| Agricultural Chemistry | 1,311.95 | |
| Drawing | 200.26 | |
| Meteorology | 129.27 | |

| | | |
|---|---|---|
| Rural Engineering | $ 1,681.57 | |
| Soil Technology | 2,067.61 | |
| Extension Department | 29,225.29 | |
| Summer school | 8,000.00 | |
| Investigation of bean production | 6,043.35 | |
| Repairs | 6,804.49 | |
| Salaries | 536,064.39 | $761,187.24 |
| Balance unexpended June 30, 1919 | | $113,550.76 |

Of this balance, about $69,850 is covered by liabilities incurred prior to June 30, 1919. The following items will lapse:

| | |
|---|---|
| Salaries | $34,201.74 |
| Additional instruction | 9,500.00 |
| | $43,701.74 |

## Circulating Fund, 1918-19

| | Balance July 1, 1918 | Credits from sales and other income | Credits, net transfers from other departments | Total credits | Debits, cash items | Debits, net transfers to other departments | Total debits | Balance June 30, 1919 |
|---|---|---|---|---|---|---|---|---|
| Administration: | $ 29.22 | $ 653.17 | $ 48.97 | $ 731.36 | $ 364.65 | ..... | $ 364.65 | $ 366.71 |
| General | 12.48 | 13.60 | 143.03 | 169.11 | 63.67 | ..... | 63.67 | 105.44 |
| Business Office | ..... | 419.32 | 39.69 | 459.01 | 346.62 | ..... | 346.62 | 112.39 |
| Publication Office | 253.37 | 1,804.00 | 1,771.22 | 3,828.59 | 3,315.57 | ..... | 3,315.57 | 513.02 |
| Engineer's Office | 138.84 | 150.35 | 180.09 | 469.28 | 283.96 | ..... | 283.96 | 185.32 |
| Grounds | 63.75 | 69.75 | ..... | 133.50 | 32.50 | ..... | 32.50 | 101.00 |
| Lockers | ..... | ..... | 180.00 | 180.00 | 144.00 | ..... | 144.00 | 36.00 |
| Salaries | 2,024.24 | 16,148.12 | 9,059.17 | 27,231.53 | 26,625.42 | ..... | 26,625.42 | 606.11 |
| Animal Husbandry | 1,166.67 | 28,651.72 | ..... | 29,818.39 | 10,265.11 | $12,469.02 | 22,734.13 | 7,084.26 |
| Dairy Industry | 514.62 | 9,014.41 | ..... | 9,529.03 | 7,274.73 | 1,215.69 | 8,490.42 | 1,038.61 |
| Poultry Husbandry | ..... | 952.27 | ..... | 952.27 | 773.97 | 59.71 | 833.68 | 118.59 |
| Entomology | 96.96 | 1,478.52 | ..... | 1,575.48 | 1,173.96 | 309.47 | 1,483.43 | 92.05 |
| Farm Crops | 1,157.90 | 17,609.67 | 6,274.54 | 25,042.11 | 20,046.30 | ..... | 20,046.30 | 4,995.81 |
| Farm Practice | 339.85 | 1,843.01 | ..... | 2,182.86 | 1,120.92 | 65.55 | 1,186.47 | 996.39 |
| Botany | 425.61 | 2,380.26 | ..... | 2,805.87 | 1,798.83 | 294.93 | 2,093.76 | 712.11 |
| Floriculture | 138.24 | 643.41 | ..... | 781.65 | 255.63 | 834.42 | 1,090.05 | *308.40 |
| Forestry | 14.67 | 69.60 | ..... | 84.27 | 7.00 | 131.17 | 138.17 | *53.90 |
| Landscape Art | 14.04 | 196.76 | 13.71 | 224.51 | 102.42 | ..... | 102.42 | 122.09 |
| Plant Breeding | 678.99 | 1,582.08 | ..... | 2,261.07 | 718.13 | 836.23 | 1,554.36 | 706.71 |
| Pomology | 89.69 | 13.28 | ..... | 102.97 | 80.04 | 14.11 | 94.15 | 8.82 |
| Farm Bureau | 3,245.60 | 44,721.20 | ..... | 47,966.80 | 38,961.33 | 1,455.06 | 40,416.39 | 7,550.41 |
| Home Economics | 70.50 | ..... | ..... | 70.50 | ..... | ..... | ..... | 70.50 |
| Rural Education | 321.98 | 250.25 | ..... | 572.23 | 167.44 | 25.06 | 192.50 | 379.73 |
| Soil Technology | | | | | | | | |
| Total | $10,707.22 | $128,664.75 | $17,710.42 | $157,172.39 | $113,922.20 | $17,710.42 | $131,632.62 | $25,539.77 |

* Indicates overdraft.

## Income Fund, 1918–19

| | Balance July 1, 1918 | First term | Second term | Third term | Fourth term | Summer school | Winter course | S. A. T. C. | Delinquent |
|---|---|---|---|---|---|---|---|---|---|
| Administration: | | | | | | | | | |
| General | $8,160.50 | $3,020.00 | $6,972.50 | $6,550.00 | $100.00 | | $375.00 | $13,550.00 | *$569.00 |
| Dean's Office | | | | | | | | | |
| Secretary's Office | 71.57 | | | | | | | | |
| Business Office | 39.36 | | | | | | | | |
| Publication Office | 89.11 | | | | | | | | |
| Library | 20.03 | | | | | | | | |
| Engineer's Office | 853.34 | | | | | | | | |
| Grounds | 65.77 | | | | | | | | |
| Salaries | | | | | | | | | |
| Animal Husbandry | | | | | | | | | |
| Dairy Industry | 730.66 | 102.00 | 617.75 | 380.15 | | | | | |
| Poultry Husbandry | 1,017.71 | | | | | | 210.00 | | 5.85 |
| Entomology | 897.98 | 176.00 | 305.00 | 863.50 | | $ 15.00 | 88.00 | | |
| Farm Crops | 704.44 | 36.00 | 248.00 | 45.00 | | 27.50 | | 79.00 | 48.50 |
| Farm Practice | 3,681.24 | | | | | 38.00 | 59.50 | | 3.00 |
| Botany | 3,493.64 | 457.92 | 923.60 | 602.27 | | | | | |
| Floriculture | 113.95 | 12.00 | 130.50 | 228.00 | | 90.50 | | 27.00 | 8.50 |
| Forestry | 52.86 | 2.50 | | 42.50 | | | 8.00 | | 2.00 |
| Landscape Art | 319.37 | 5.00 | 10.00 | 29.00 | | | | 4.00 | 1.00 |
| Plant Breeding | 56.59 | 12.00 | 3.00 | 15.00 | | 3.00 | | 2.00 | 4.50 |
| Plant Pathology | 1,064.12 | 54.19 | 269.90 | 291.94 | | | 4.50 | | 13.00 |
| Pomology | 132.25 | 38.50 | | 237.50 | | | 12.00 | 3.00 | 6.00 |
| Farm Management | 330.78 | 11.00 | 52.50 | 36.00 | | | | 3.50 | 5.50 |
| Home Economics | 1,281.98 | 1,853.00 | 1,855.75 | 1,671.00 | | | 39.00 | 2.00 | 4.00 |
| Rural Economy | | | | | | 503.00 | 95.00 | | 29.00 |
| Rural Education | 14.97 | | | 6.00 | | | | | |
| Rural Organization | | | | | | | | | |
| Agricultural Chemistry | 209.80 | | | | | | | | |
| Meteorology | 92.84 | 12.00 | 88.00 | 40.00 | | | | 86.54 | 2.00 |
| Rural Engineering | 142.62 | 28.00 | 32.00 | 277.00 | | 10.00 | 20.00 | 12.00 | 11.00 |
| Soil Technology | 1,297.69 | 9.00 | 92.43 | 112.50 | | | | | 13.77 |
| Extension Department | 1,778.38 | | | | | | | | |
| Summer school tuition | | | | | | 2,161.30 | | | |
| Total | $26,714.45 | $5,829.11 | $11,600.93 | $11,427.36 | $100.00 | $2,848.30 | $911.00 | $13,769.04 | *$726.62 |

* Including $544 reinstatement fees and student fines.

## Income Fund, 1918–19 (*concluded*)

| | Total fees | Credits, cash items | Credits, net transfers from other departments | Total credits | Debits, cash items | Debits, net transfers to other departments | Total debits | Balance June 30, 1919 |
|---|---|---|---|---|---|---|---|---|
| Administration: | $31,136.50 | $2,583.81 | ..... | $41,880.81 | $6,837.00 | $15,613.65 | $22,451.55 | $19,429.26 |
| General | ..... | ..... | $ 300.00 | 300.00 | ..... | ..... | ..... | 300.00 |
| Dean's Office | ..... | 25.00 | 104.70 | 201.27 | 122.43 | ..... | 122.43 | 78.84 |
| Secretary's Office | ..... | 32.83 | 556.46 | 628.65 | 312.57 | ..... | 312.57 | 316.08 |
| Business Office | ..... | 252.62 | 803.30 | 1,145.03 | 769.50 | ..... | 769.50 | 375.53 |
| Publication Office | ..... | 450.00 | 991.18 | 1,462.11 | 540.43 | ..... | 540.43 | 921.68 |
| Library | ..... | 100.92 | 2,253.18 | 3,207.44 | 2,113.19 | ..... | 2,113.19 | 1,094.25 |
| Engineer's Office | ..... | ..... | 910.15 | 975.92 | 956.26 | ..... | 956.26 | 19.66 |
| Grounds | ..... | ..... | 1,235.00 | 1,235.00 | 1,196.95 | ..... | 1,196.95 | 38.05 |
| Salaries | ..... | ..... | 3,429.77 | 3,429.77 | 2,060.39 | ..... | 2,060.39 | 1,369.38 |
| Animal Husbandry | ..... | ..... | 806.42 | 2,852.83 | 1,723.40 | ..... | 1,723.40 | 1,129.43 |
| Dairy Industry | 1,315.75 | 656.90 | 2,367.46 | 4,145.07 | 2,454.99 | ..... | 2,454.99 | 1,690.08 |
| Poultry Husbandry | 103.00 | 35.86 | ..... | 2,433.34 | 1,257.35 | 93.25 | 1,350.60 | 1,082.74 |
| Entomology | 1,499.50 | 125.34 | ..... | 1,259.28 | 471.53 | 322.93 | 794.46 | 464.82 |
| Farm Crops | 429.50 | 326.05 | 1,233.92 | 5,241.21 | 5,095.01 | ..... | 5,095.01 | 146.20 |
| Farm Practice | ..... | ..... | ..... | 5,603.43 | 2,101.45 | 335.72 | 2,437.17 | 3,166.26 |
| Botany | 2,109.79 | ..... | 82.49 | 576.94 | 203.41 | ..... | 203.41 | 373.53 |
| Floriculture | 380.50 | ..... | 112.54 | 215.40 | 45.69 | ..... | 45.69 | 169.71 |
| Forestry | 50.00 | ..... | ..... | 372.87 | 11.95 | 225.16 | 237.11 | 135.76 |
| Landscape Art | 53.50 | ..... | 711.17 | 816.51 | 749.06 | ..... | 749.06 | 67.45 |
| Plant Breeding | 47.50 | 1.25 | ..... | 2,019.04 | 1,510.30 | 48.49 | 1,558.79 | 460.25 |
| Plant Pathology | 637.03 | 317.89 | ..... | 417.25 | 83.39 | 11.54 | 94.93 | 322.32 |
| Pomology | 285.00 | ..... | ..... | 497.54 | 225.69 | 40.10 | 265.79 | 231.75 |
| Farm Management | 144.50 | 22.26 | 378.88 | 9,268.59 | 8,382.73 | ..... | 8,382.73 | 885.86 |
| Home Economics | 6,006.75 | 1,600.98 | 367.54 | 470.87 | 325.25 | ..... | 325.25 | 145.62 |
| Rural Economy | ..... | 103.33 | 38.16 | 180.75 | 115.79 | ..... | 115.70 | 65.05 |
| Rural Education | 6.00 | 121.62 | 23.60 | 23.60 | 22.72 | ..... | 22.72 | 0.88 |
| Rural Organization | ..... | ..... | ..... | 209.80 | 100.75 | 56.33 | 157.08 | 52.72 |
| Agricultural Chemistry | ..... | ..... | 102.09 | 423.47 | 192.98 | ..... | 192.98 | 230.49 |
| Meteorology | 228.54 | ..... | 656.75 | 1,891.29 | 1,234.52 | ..... | 1,234.52 | 656.77 |
| Rural Engineering | 390.00 | 701.92 | ..... | 1,678.52 | 826.25 | 157.68 | 983.93 | 694.59 |
| Soil Technology | 227.70 | 153.13 | ..... | 9,777.14 | 4,551.08 | 656.82 | 5,207.90 | 4,569.24 |
| Extension Department | ..... | 7,998.76 | ..... | 2,161.30 | 2,000.97 | 3.09 | 2,004.06 | 157.24 |
| Summer school tuition | 2,161.30 | ..... | ..... | | | | | |
| Total | $47,212.36 | $15,610.47 | $17,464.76 | $107,002.04 | $48,595.79 | $17,564.76 | $66,160.55 | $40,841.49 |

**State Deficiency Appropriation, 1917–18**

| | |
|---|---|
| Appropriation for fuel, light, power, and water | $19,000.00 |
| Expenditures previously reported | 12,189.23 |
| Balance unexpended July 1, 1918 | $6,810.77 |
| Expenditures subsequent to July 1, 1918, on liabilities incurred prior to that date | $6,600.36 |
| Balance of appropriation lapsed | $210.41 |

**State Deficiency Appropriation, 1918–19**

| | |
|---|---|
| Appropriation for extension travel, printing, and lectures | $8,000.00 |
| Expended to June 30, 1919 | 6,831.80 |
| Balance unexpended June 30, 1919 | $1,168.20 |

This balance is covered by liabilities incurred prior to June 30, 1919.

**State Deficiency Appropriation, 1919**

| | |
|---|---|
| Appropriation for fuel, light, power, and water | $2,500.00 |
| Expended to June 30, 1919 | 2,005.38 |
| Balance unexpended June 30, 1919 | $494.62 |

This balance is covered by liabilities incurred prior to June 30, 1919.

**State Appropriation for Game Farm, 1917**

| | |
|---|---|
| Appropriation | $15,000.00 |
| Expenditures previously reported | 13,893.40 |
| Balance unexpended July 1, 1918 | $1,106.60 |
| Expenditures subsequent to July 1, 1918, on liabilities incurred prior to that date | 1,014.99 |
| Balance of appropriation lapsed | $91.61 |

**State Appropriation for Game Farm, 1918–19**

| | | |
|---|---|---|
| Appropriation | | $10,615.00 |
| Expended to June 30, 1919: | | |
| Salaries | $2,633.71 | |
| General expense | 4,645.63 | 7,279.34 |
| Balance unexpended June 30, 1919 | | $3,335.66 |

Of this balance, $2,429.37 is covered by liabilities incurred prior to June 30, 1919. Salaries, $906.29, will lapse.

**State Appropriation for the Investigation of Bean Production, 1917**

| | |
|---|---|
| Appropriation | $8,500.00 |
| Expenditures previously reported | 7,415.56 |
| Balance unexpended July 1, 1918 | $1,084.44 |
| Expenditures subsequent to July 1, 1918, on liabilities incurred prior to that date | 1,082.94 |
| Balance of appropriation lapsed | $1.50 |

**Smith-Hughes Fund, 1918–19**

| | |
|---|---|
| Overdraft July 1, 1918 | $ 2,690.33 |
| Expenditures to June 30, 1919 | 11,510.31 |
| | $14,200.64 |
| Receipts to June 30, 1919 | 12,376.45 |
| Overdraft June 30, 1919 | $1,824.19 |

This overdraft represents an advance by the University for the expenditures from April 1 to June 30, for which reimbursement will be made by the New York State Department of Education.

**Mess Hall Fund, 1918–19**

| | |
|---|---|
| Receipts to June 30, 1919 | $45,257.10 |
| Expenditures to June 30, 1919 | 45,257.10 |

**Federal Extension (Smith-Lever Fund)**

| | |
|---|---|
| Total amount appropriated to the New York State College of Agriculture for the fiscal year 1918–19 | $92,049.52 |

**Federal Research (Hatch and Adams Funds)**

| | |
|---|---|
| Total amount appropriated to the New York State College of Agriculture for the fiscal year 1918–19 | $27,000.00 |

**Federal Teaching (Morrill and Nelson Funds)**

| | |
|---|---|
| Total amount appropriated to the New York State College of Agriculture for the fiscal year 1918–19 | $20,000.00 |

## Conclusion

The preceding pages briefly summarize the work of the New York State College of Agriculture during the year 1918–19. There are two principal points which might well be emphasized. One is that this year saw the end of war activities devoted to the successful termination of the contest with the Central Powers of Europe, and the beginnings of a new era which necessarily carries with it many problems of reconstruction and readjustment. The other point, which I would wish particularly to emphasize, is the need for a more flexible budget, which will permit the College to do effectively the work which the State requires of it. The institution must have release from a fiscal domination that cripples educational advancement. The work which the College has been doing, and the part which it has been able to take in rendering service to the State and in educating students at the College, represents a distinct achievement. But it represents only a part of what might have been done with the same amount of money had the institution been free to expend that money in accordance with its own knowledge of the work to be done rather than in accordance with an inflexible appropriation.

Respectfully submitted,

A. R. MANN,

*Dean, New York State College of Agriculture.*

AUGUST, 1918 MEMOIR 13

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# CHLOROPHYLL INHERITANCE IN MAIZE

E. W. LINDSTROM

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# CHLOROPHYLL INHERITANCE IN MAIZE

# CHLOROPHYLL INHERITANCE IN MAIZE[1]

E. W. Lindstrom

Mendelian inheritance and chlorophyll have enjoyed an interesting and intimate relation in the field of genetics. Green and yellow cotyledons in Pisum, a definite chlorophyll character, ushered in this relation at the time of Mendel and furnished in part the material for his classical researches on inheritance. And then in the early part of the twentieth century, after the rediscovery of Mendelism, when Mendelian phenomena were accused of being restricted to superficial and unessential characters such as flower, plumage, and coat color, the discovery of Mendelian inheritance of such a vital character as chlorophyll in many other species (Antirrhinum, Melandrium, Mirabilis) aided in dispelling this misconception.

Later, when apparent cases of non-Mendelian inheritance were widely quoted, chlorophyll characters again played an important rôle. For example, green and white variegation in Pelargonium was cited as an excellent case of non-Mendelian inheritance, until the sectorial and periclinal chimera explanation eliminated such irregular phenomena from the controversy.

Since then, Mendelian inheritance of chlorophyll has been substantiated in numerous genera, and now there is no doubt as to the extension of Mendelian laws to govern the inheritance of this pigment.

The modern tendency in genetics seems to be toward an attempt to correlate the genetic behavior of chlorophyll with its chemistry and its physiology. This has already been accomplished to a limited degree with another pigment, anthocyan, to the advantage of both chemistry and genetics.

Chemical and physiological research has demonstrated a surprising complexity of the pigment chlorophyll. The chlorophyll molecule has, however, been resolved into a series of simpler components. Also, physiological interrelations between chlorophyll and its allied pigments xanthophyll and carotin have already been suggested. It remains for the geneticist to make an intensive genetic study of chlorophyll to aid in these researches.

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[1] Paper No. 65, Department of Plant Breeding, Cornell University, Ithaca, New York.

Beginning with the classical studies on the inheritance of chlorophyll by Gregor Mendel in 1865, there has developed a long series of researches on the genetics of this pigment. These investigations have shown that chlorophyll inheritance in a large number of genera, as Antirrhinum, Aquilegia, Hordeum, Lunaria, Lycopersicum, Melandrium, Mirabilis, Pelargonium, Phaseolus, Pisum, Plantago, Secale, Senecio, Urtica, and Zea, can be explained on a Mendelian basis.

With a few exceptions, the abnormal, or mutant, types of chlorophyll characters have proved to be simple Mendelian recessives to normal green. These exceptions include, curiously enough, Mendel's yellow cotyledons in Pisum which proved to be dominant to the green (a recessive yellow cotyledonous type was found by White [1916]); Baur's (1907) aurea type, which was found to be due to the hybrid condition of a green-yellow pair of chlorophyll factors; and Trow's (1916) case in Senecio, in which certain albino seedlings were due to a double recessive condition of two chlorophyll factors.

More definite chlorophyll factors have been determined in the genus Zea than in any other genus. To date at least eight such factors have been isolated and genetically tested. Six of these have already been described in previous publications; two are seedling factors, and the other four are concerned with the chlorophyll development in the mature plant (East and Hayes, 1911; Emerson, 1912; Gernert, 1912; Miles, 1915). In addition another seedling factor has been discovered by the writer, and another striping factor has been added to the series.

The genetic interrelations between these eight factors, and their relation to other maize factors such as aleurone color, form the basis for this study.

## MATERIAL AND METHODS

The pedigree cultures from which these studies were begun were furnished by Professor R. A. Emerson in 1914. Mr. F. C. Miles, then working under Professor Emerson at the University of Nebraska, had commenced the investigation of some of these chlorophyll problems, and they were all transferred to the writer at that time. It is with gratitude that the writer acknowledges his indebtedness to Professor Emerson, who has been a constant source of inspiration in the work.

All pollinating was carefully controlled, bags of extra heavy manila, of good quality, having been used in the work. Only one pollination to an ear was made, in order to diminish the chances of contamination. In self- or cross-pollination, the tassel bag (12 pounds) holding the pollen was quickly and carefully substituted for the ear bag (4 pounds), which had been securely tied over the ear before the silks emerged. The hands and the forearms were washed in a 50- to 60-per-cent solution of alcohol between pollinations. Every pollination was recorded on an individual tag, tied with the bagged ear. Individual pedigree notes were taken of the plants in the field, permanent stakes having been set at planting time for this purpose. In labeling crosses the system was followed of always writing the female parent first.

During the winter extensive plantings were made in the greenhouse to determine the seedling inheritance. The seeds were planted in flats, and counts and descriptions were made within two or three weeks after planting. In the large majority of cases the segregation of the various seedling types proved to be exceptionally distinct, because the environment was very uniform, during the winter months, in regard to light, temperature, moisture, and soil.

Probable errors and closeness of fit were determined wherever necessary. The formula used for probable error of a Mendelian ratio is

$$\text{P. E.} = 0.6745\sqrt{pqn},$$

in which $p$ and $q$ are the two elements in a ratio, as 3 and 1, 15 and 1, 1 and 1, and so forth, and $n$ is the total number of individuals in the experiment. The probable error determined from this formula is compared with the actual deviation from the theoretical expectancy.

In calculating the closeness of fit, the method described by Elderton (1901) was used. In this method, the goodness of fit of theory and observation is expressed by $P$, a measure on the scale of 0 to 1 of the probability that the deviations from the theoretical frequencies may be reasonably supposed to be due to errors of random sampling (Harris, 1912). In some cases in this paper, when the closeness of fit is very good and the value for $P$ is not given in Elderton's tables, the value for $\chi^2$ is given. When $\chi^2$ is less than 1, theory and observation agree very well.

SEEDLING INHERITANCE

*Description of types*

*White.*— Seedlings of the white type are true albinos, lacking absolutely all green color. They are apparently devoid of all chloroplasts. In some cases a faint tinge of yellow appears in the leaves, but this is thought to be caused merely by the gradual aging of the tissue.

As soon as the food in the seed is exhausted, these white seedlings perish. The duration of their life varies from one to three weeks after germination.

Carbohydrate feeding of this type under sterile conditions proved of no avail in lengthening the life of the seedlings. Feeding them nutrient solutions with excess of iron or magnesium produced no effect.

These white seedlings have been described also by Emerson (1912), Gernert (1912), and Miles (1915).

*Virescent-white* (Plate I).— The virescent-white type usually begins as a pure white seedling, but under favorable conditions it gradually assumes a yellowish green color within a week, especially at the tips of the newer leaves. Gradually the color becomes a deeper green, and eventually the plant may become normally green altho it is usually much smaller than a normal plant. Virescent-white plants that have turned green usually show a few characteristic narrow white streaks or stripes in some of the leaves. Mature seed has been obtained from such plants, altho it is difficult to procure many ripened ears.

There is often a considerable range of color in this type. Some seedlings begin with more green than others, and are really greenish white rather than yellow or yellowish green. Others begin practically pure white and retain this color for several weeks, showing only a faint suggestion of green on the leaf tips. There are all gradations between these limits, but genetically they behave as a unit. It may be that these slight differences are due to multiple allelomorphs of the virescent factor. Because of the influence of the immediate environment on the phenotypic expression of this type, such variations are not easily isolated and studied.

Temperature and light exert a marked influence on the virescent-white type. Growing the virescent-white seedlings in a low temperature or in poor light tends to suppress the development of the green color. Full sunlight, and especially high temperature (from 90° to 110° F.), markedly

YELLOW TYPE (LEFT) AND VIRESCENT-WHITE TYPE (RIGHT)

Seedlings three weeks old

accelerate the appearance of the green pigment. Excess of iron or magnesium appears to have no effect on the color.

These virescent-white seedlings were described by Miles (1915) as yellowish-whites.

*Yellow* (Plate I).— The new yellow type was isolated by the writer from a culture of heterozygous green plants. Certain of these green plants were found to produce seventy-five per cent green and twenty-five per cent yellow seedlings when self-pollinated. Miles (1915) apparently included this type among his yellowish-whites, for one of his color illustrations (4 b) suggests the yellow type of seedling.

The color in the early seedling stage is a clear lemon yellow (Ridgway's, Pinard Yellow). There is of course some range of color, due mostly to the effect of light and temperature, but the gradations behave as a single unit in inheritance.

Under favorable conditions this yellow type also will gradually assume a greenish color. The virescent nature, however, is not nearly so marked as in the virescent-white type. In fact, the writer has never been able to mature a yellow seedling.

The yellow pigment in this type closely resembles xanthophyll. It is insoluble in water and weak alcohol, but readily dissolves in strong solutions of ethyl alcohol (95 per cent).

### *Inheritance of the three seedling types*

*White.*— The albino type of maize has been shown by Emerson (1912) and Gernert (1912) to be a simple Mendelian recessive to normal green. In addition to the counts reported by these investigators, the following results have been obtained by self-pollinating green plants heterozygous for white, and growing the seedling progenies: green seedlings, 1513 (1551); white seedlings, 555 (517). The theoretical numbers are given in parenthesis. Obviously this is a simple 3:1 ratio $\left(\frac{\text{Dev.}}{\text{P. E.}} = 2.9\right)$.

*Virescent-white.*— In addition to the results reported by Emerson and Miles, the following data have been accumulated from self-pollinating heterozygous green plants: green seedlings, 4297 (4268); virescent-white seedlings, 1394 (1423). Here again there is a simple Mendelian ratio $\left(\frac{\text{Dev.}}{\text{P. E.}} = 1.3\right)$.

Twelve ears of virescent-whites that had turned green and were self-fertilized produced a total of 717 virescent-white seedlings and 9 greens. The latter were due without doubt to stray pollen grains. These data prove that the virescent-white type is a simple recessive to normal green.

*Yellow.*— A third recessive seedling type is the yellow. When certain heterozygous green plants are self-fertilized, the seedling progenies exhibit distinct 3:1 ratios of green to yellow seedlings. A list of such progenies is presented in table 1:

TABLE 1. SEEDLING PROGENIES OF SELF-FERTILIZED, HETEROZYGOUS GREEN PLANTS

| Pedigree no. | Green seedlings | Yellow seedlings | Dev. | P. E. | $\frac{\text{Dev.}}{\text{P. E.}}$ |
|---|---|---|---|---|---|
| 3390— 1 | 98 | 24 | 6.5 | 3.2 | 2.0 |
| — 2 | 110 | 39 | 1.8 | 3.6 | 0.5 |
| 3397— 7 | 50 | 44 | 20.5 | 2.8 | 7.3 |
| 3432— 2 | 68 | 18 | 3.5 | 2.7 | 1.3 |
| — 3 | 42 | 13 | 0.8 | 2.2 | 0.4 |
| 3861— 3 | 54 | 17 | 0.8 | 2.5 | 0.3 |
| — 4 | 141 | 38 | 6.8 | 3.9 | 1.7 |
| — 6 | 120 | 30 | 7.5 | 3.6 | 2.1 |
| — 8 | 27 | 9 | 0.0 | 1.8 | 0.0 |
| — 9 | 70 | 21 | 1.8 | 2.8 | 0.6 |
| —10 | 39 | 14 | 0.7 | 2.1 | 0.3 |
| —12 | 85 | 26 | 1.8 | 3.1 | 0.6 |
| —15 | 76 | 16 | 7.0 | 2.8 | 2.5 |
| 3866— 2 | 71 | 31 | 5.5 | 2.9 | 1.9 |
| — 5 | 114 | 74 | 27.0 | 4.0 | 6.8 |
| 3871— 1 | 26 | 10 | 1.0 | 1.8 | 0.6 |
| — 2 | 122 | 39 | 1.3 | 3.7 | 0.3 |
| — 3 | 37 | 11 | 1.0 | 2.0 | 0.5 |
| — 4 | 98 | 41 | 6.3 | 3.4 | 1.8 |
| 3872— 1 | 45 | 17 | 1.5 | 2.3 | 0.7 |
| Total | 1,493 | 532 | 26.0 | 13.1 | 2.0 |
| Theoretical (3:1) | 1,519 | 506 | ..... | ..... | ..... |

*Genetic factors for the seedling types*

It has become necessary to revise the system inaugurated by Miles (1915), of using *Aa* and *Bb* to denote the two factor pairs involved in seedling inheritance. These letters have been used in other phases

of the corn investigations by Professor Emerson. Consequently the following series of symbols has been devised:

*Ww* — factor pair for the green-white relation
*Vv* — factor pair for the green-virescent-white relation
*Ll* — factor pair for the green-yellow relation

It will be noted that the factors for all these types (or mutants) are named from the recessive condition. The letter *l* stands for the Latin *luteus*, meaning yellow.

*Interrelation between the white and virescent-white types*

Miles (1915) has reported on the inheritance of the white and virescent-white types, and has suggested an hypothesis to explain their genetic interrelation. For a complete discussion of this, the reader is referred to Miles' article. It is necessary only to repeat that the factorial composition of these types was determined to be as follows:

Normal green — *W W V V*
Virescent-white — *W W v v*
White — *w w V V* and *w w v v*

When green plants that produced 25 per cent whites (*W w V V*) were crossed by greens heterozygous for the *V* factor (*W W V v*), the $F_1$ plants were all fully green, showing that the two types were genetically distinct. When these green $F_1$ plants were self-fertilized, it was seen that there were four kinds of $F_2$ seedling progenies, as was to be expected on the hypothesis. Also, they occurred in approximately a 1:1:1:1 proportion.

Additional material from these crosses has been grown since Miles reported on them. The detailed data are presented in table 2A, given in the appendix (page 64). Here the $F_2$ progenies are listed individually, and they exhibit a fair approximation to the theoretical expectation. A summary of these progenies has been arranged in table 2 (page 14).

The four kinds of $F_1$ plants are very evident from this table, and they occur in almost equal proportions. The closeness of fit has been determined for the distribution, and the value of *P* is 0.348. Thus the chances are approximately 2 to 1 that deviations as great as those obtained are not due merely to errors of random sampling. In other words, theory and observation agree only fairly well.

The slight excess of the homozygous green class is almost to be expected, since it has been observed that plants heterozygous for the *W* factor are slightly less vigorous than normal green plants. When selfing $F_1$ plants in the field, there is a natural tendency to pollinate the more vigorous plants in greater numbers.

In this connection it is interesting to note a general correlation between chlorophyll factors and plant growth. In all the material in which the *w* factor is concerned, the plants show a tendency toward producing only a single stalk which finds great difficulty in standing up in a strong wind. It is only rarely that a sucker is produced. This correlation or physiological effect of the *w* factor has not as yet been fully studied.

TABLE 2. SUMMARY OF $F_2$ SEEDLING PROGENIES OF THE CROSS W w V V x W W V v

| Pedigree nos. | W W V V All green | W W V v 3 green, 1 virescent-white | W w V V 3 green, 1 white | W w V v 9 green, 3 virescent-white, 4 white |
|---|---|---|---|---|
| 3008— 3 x 3004—18 | 5 | 3 | 3 | 1 |
| — 6 x —18 | 5 | 3 | 5 | 4 |
| —19 x 3005— 3 | 8 | 5 | 2 | 5 |
| —33 x 3004—10 | 3 | 3 | 3 | 2 |
| Total | 21 | 14 | 13 | 12 |
| Theoretical (1:1:1:1) | 15 | 15 | 15 | 15 |
| Closeness of fit (P) for total | | | | P = 0.3484 |

Before leaving this series of four crosses, it may be mentioned that twenty-one of the $F_1$ plants listed in table 2 A have been self-pollinated and the $F_3$ progenies grown, and six others have been crossed with other types. But inasmuch as they fully confirm the hypothesis, their publication is scarcely deemed necessary.

An interesting check on the genetic relation of the *w* and *v* factors is seen in crosses of green plants heterozygous for the *W* factor, by virescent-white plants that turned green. Such crosses give in $F_1$ a progeny that is entirely green, as is seen from table 3.

This, of course, is merely another indication of the genetic difference between the white and virescent-white types, for the male parent in these crosses was a pure virescent-white.

TABLE 3. $F_1$ SEEDLING PROGENIES OF THE CROSS W wV V x W W v v

| Pedigree nos. | Green seedlings |
|---|---|
| 812— 4 x 706—26 | 49 |
| 1180— 6 x —24 | 71 |
| — 7 x — 3 | 19 |
| —15 x — 3 | 142 |
| —24 x — 5 | 34 |
| Total | 315 |

The data presented above, together with the 9:3:4 ratios in table 2 A, indicate that the factors *W* and *V* are independently inherited. The total results of the $F_2$ seedling progenies giving these 9:3:4 ratios are as follows:

Observed: 640 green: 190 virescent-white: 268 white
Calculated: 618 green: 206 virescent-white: 274 white

The closeness of fit is not exceptionally good, *P* having a value of 0.345. Nevertheless there is no suggestion of a linkage in this distribution, and, while a very weak linkage might give a slightly better fit than the one shown above, it seems unreasonable to suppose that there is such a linkage. Unfortunately a backcross cannot be used to test for a linkage, since the double recessive is not viable.

*Interrelation between the virescent-white and yellow types*

It has been shown that both the virescent-white type and the yellow type are simple recessive to normal green. How do they react with each other? To determine this, several of the heterozygous plants shown in table 1, and some others from different sources, were crossed with certain virescent-white plants that had turned green. In most cases it was impossible to self the male parent because of its poor vigor. In one case in which this was possible (3858—2), the progeny was 100 per cent virescent-white seedlings, showing the recessive nature of the male parent. The $F_1$ results of these crosses are arranged in table 4.

The distinct 1:1 ratio in $F_1$ suggests immediately a different interrelation from that between white and virescent-white. In fact, thus far it might appear as if there were no genetic difference between the *V* and *L* factors.

In the $F_1$ virescent-white seedlings, however, there was absolutely no trace of the yellow pigment of the female parent. The green seedlings were perfectly normal dark green. It is evident that the proportion of the two types shown in table 4 approaches very closely a 1:1 ratio.

TABLE 4. $F_1$ SEEDLING PROGENIES FROM THE CROSS OF GREEN PLANTS HETEROZYGOUS FOR YELLOW SEEDLINGS BY HOMOZYGOUS VIRESCENT-WHITES

| Pedigree nos. of parents | Pedigree no. of $F_1$ | Green seedlings | Virescent-white seedlings |
|---|---|---|---|
| 3861— 3 x 3858—2 | 826 | 47 | 49 |
| —14 x —8 | 832 | 60 | 57 |
| 3866— 6 x —6 | 837 | 91 | 87 |
| 3871— 1 x —5 | 846 | 76 | 85 |
| — 2 x —7 | 847 | 77 | 82 |
| — 3 x —5 | 848 | 87 | 82 |
| 3872— 1 x —3 | 849 | 83 | 81 |
| Total | | 521 | 523 |
| Theoretical (1:1) | | 522 | 522 |

In another set of crosses one parent was heterozygous for the *V* factor while the other parent was heterozygous for the *L* factor. The $F_1$ seedling progenies from this series of crosses are given in table 5:

TABLE 5. $F_1$ SEEDLING PROGENIES FROM THE CROSS OF GREEN PLANTS HETEROZYGOUS FOR YELLOW SEEDLINGS (Ll) BY GREEN PLANTS HETEROZYGOUS FOR VIRESCENT-WHITE SEEDLINGS (Vv)

| Pedigree nos. of parents | Pedigree no. of $F_1$ | Green seedlings | Virescent-white seedlings | Dev. | P. E. | Dev./P. E. |
|---|---|---|---|---|---|---|
| 3861—10 x 3924— 4 | 827–828 | 71 | 17 | 5.0 | 2.7 | 1.9 |
| —12 x — 4 | 829–830 | 70 | 23 | 0.3 | 2.8 | 0.1 |
| 3924— 4 x 3861—12 | 882–883 | 108 | 38 | 1.5 | 3.5 | 0.4 |
| Total | | 249 | 78 | 3.8 | 5.3 | 0.7 |
| Theoretical (3:1) | | 245 | 82 | ..... | ..... | ..... |

Here again the same interrelation obtains as was seen in table 4, except that in this case the $F_1$ ratio approaches 3:1. In these seedlings also

there was no trace of the yellow color, all the non-green seedlings being truly virescent-white. In table 5 reciprocal crosses give identical results.

A large $F_2$ generation was produced by self-fertilizing many of the green plants, and a few of the virescent-whites that turned green, listed in the $F_1$ tables 4 and 5. The seedlings from these selfed $F_1$ plants were grown in the greenhouse and counts were made of the $F_2$ seedlings. The data obtained from the $F_1$ plants used in table 4 are presented in table 6:

TABLE 6. $F_2$ SEEDLING PROGENIES OF SELF-FERTILIZED $F_1$ PLANTS LISTED IN TABLE 4

| Pedigree no. | From $F_1$ greens | | | From $F_1$ virescent-whites | | |
|---|---|---|---|---|---|---|
| | Green seedlings | Virescent-white seedlings | Yellow seedlings | Pedigree no. | Virescent-white seedlings | Yellow seedlings |
| 826— 1 | 68 | 11 | 5 | 826—10 | 42 | 7 |
| — 3 | 314 | 81 | 12 | —14 | 27 | 12 |
| — 6 | 22 | 3 | 3 | —12 x —8 | 83 | 26 |
| — 8 | 105 | 21 | 8 | | | |
| —18 | 63 | 16 | 4 | | | |
| —19 | 64 | 15 | 6 | | | |
| —20 | 51 | 16 | 6 | | | |
| —22 | 64 | 14 | 2 | | | |
| —23 | 82 | 26 | 8 | | | |
| —25 | 83 | 11 | 9 | | | |
| —27 | 73 | 21 | 6 | | | |
| —29 | 72 | 20 | 10 | | | |
| —34 a | 52 | 15 | 3 | | | |
| —37 | 130 | 22 | 8 | | | |
| —38 | 184 | 32 | 11 | | | |
| —5 x —2 | 61 | 18 | 4 | | | |
| 832— 1 | 170 | 45 | 7 | | | |
| — 5 | 58 | 19 | 5 | | | |
| — 7 | 46 | 13 | 6 | | | |
| —10 | 47 | 6 | 7 | | | |
| —12 | 110 | 26 | 1 | | | |
| —15 | 60 | 26 | 0 | | | |
| 837— 5 | 36 | 9 | 3 | 837— 2 | 45 | 12 |
| — 8 | 24 | 10 | 4 | | | |
| — 9 | 42 | 14 | 2 | | | |
| —10 | 37 | 12 | 4 | | | |
| —12 | 36 | 7 | 4 | | | |
| 846— 1 | 33 | 9 | 2 | | | |
| — 4 | 177 | 50 | 14 | | | |
| — 7 | 173 | 48 | 15 | | | |
| — 8 | 28 | 9 | 4 | | | |

TABLE 6 (*concluded*)

| Pedigree no. | From $F_1$ greens | | | From $F_1$ virescent-whites | | |
|---|---|---|---|---|---|---|
| | Green seedlings | Virescent-white seedlings | Yellow seedlings | Pedigree no. | Virescent-white seedlings | Yellow seedlings |
| 846—10 | 148 | 31 | 11 | ..... | ..... | ..... |
| —14 | 60 | 9 | 6 | ..... | ..... | ..... |
| —16 | 47 | 9 | 4 | ..... | ..... | ..... |
| 847— 8 | 46 | 11 | 5 | 847—11 | 82 | 27 |
| —10 | 49 | 7 | 3 | —12 | 2 | 1 |
| | | | | —14 x —3 | 40 | 9 |
| 848— 5 | 128 | 22 | 10 | ..... | ..... | ..... |
| — 6 | 122 | 24 | 5 | ..... | ..... | ..... |
| —11 | 120 | 25 | 14 | ..... | ..... | ..... |
| —14 | 4 | 1 | 0 | ..... | ..... | ..... |
| —16 | 38 | 10 | 3 | ..... | ..... | ..... |
| 849— 3 | 41 | 6 | 5 | 849—6 | 31 | 9 |
| — 7 | 135 | 36 | 8 | ..... | ..... | ..... |
| —11 | 54 | 15 | 3 | ..... | ..... | ..... |
| —17 | 26 | 2 | 0 | ..... | ..... | ..... |
| Total | 3,583 | 853 | 260 | Total | 352 | 103 |
| Theoretical (12:3:1) | 3,522 | 881 | 293 | Theoretical (3:1) | 341 | 114 |
| Closeness of fit (P) for total..... P = 0.0606 | | | | $\frac{\text{Dev.}}{\text{P. E.}}$ for total..... $\frac{10.75}{6.23} = 1.7$ | | |

In this $F_2$ generation the yellow type reappeared in its original typical color. The segregation between the green, the virescent-white, and the yellow seedlings was definite and unmistakable in the large majority of the progenies.

It is easily seen that, with the exception of two progenies, all the selfed green $F_1$ plants produced seedlings of three types — green, virescent-white, and yellow — in definite proportions, which permits averaging. A total result of 3583 greens, 853 virescent-whites, and 260 yellows, suggests a 12:3:1 ratio, with which the actual results are not in very close agreement, $P$ having a value of 0.0606. One reason for the poor agreement is the presence of the three progenies 826—3, 832—12, and 832—15, in which the ratio between the virescent-white and the yellow seedlings

is nearer 15:1 than 3:1 (total 133:13). Another series of crosses has also given a suggestion of a 15:1 ratio in respect to the *L* factor (table 8, page 21), but a detailed report of this condition is withheld until more evidence will have been accumulated.

Six of the virescent-white $F_1$ plants that turned green were self-fertilized, and four were intercrossed. Their progenies consisted of seedlings which were all non-green but which did exhibit a ratio of 3 virescent-white seedlings to 1 yellow (table 6). The segregation seemed less distinct than in the case of the progenies from the green $F_1$ plants, but counts could always be made under favorable conditions of light and temperature.

This definite reappearance of the yellow type in $F_2$ suggests that the two seedling factors *L* and *V* are genetically distinct. This is further substantiated by numerous other crosses and various intercrosses of the $F_2$ plants, which are presented later.

A 12:3:1 ratio in which the *L* and *V* factors are involved can perhaps best be explained by assigning the following formulae to the various types:

Virescent-white —*LLvv*
Yellow —*llvv*
Green —*llVV* and *LLVV*

The crosses in table 4 would then be represented as *llVv* x *LLvv*. The $F_1$ plants would be of two sorts, *LlVv* and *Llvv*, or 50 per cent green and 50 per cent virescent-white. In $F_2$ all the green $F_1$ plants should give 12:3:1 ratios, while the non-green $F_1$ plants should give progenies of 3 virescent-whites to 1 yellow. Such was the condition in table 6, as is readily seen.

The crosses in table 5 could be written as *llVv* x *LLVv*. In $F_1$ two types, green and virescent-white, should occur in a 3:1 proportion. Actual results confirm this. On self-fertilizing these $F_1$ plants, the progenies from the green plants should be of two sorts, one being 100 per cent green and the other giving a 12:3:1 ratio. The latter sort should occur twice as often as the former. Do the actual data check up with the hypothesis? A summary of these $F_2$ progenies is arranged in table 7; the detailed results are listed in table 7 A, in the appendix (page 66).

The 58 green $F_1$ plants that were self-fertilized exhibited an unusually close approximation to the theoretical 1:2 proportion, there being

18 progenies of fully green seedlings and 40 progenies segregating into the three seedling classes.

TABLE 7. SUMMARY OF $F_2$ SEEDLING PROGENIES OF THE SELF-FERTILIZED GREEN $F_1$ PLANTS LISTED IN TABLE 5

(Parental formulae, l l V v x L L V v and reciprocal)

| Pedigree no. | L l V V Progenies all green | L l V v Progenies segregating into green: virescent-white: yellow |
|---|---|---|
| 829 | 3 | 3 |
| 830 | 6 | 10 |
| 882 | 5 | 15 |
| 883 | 4 | 12 |
| Total | 18 | 40 |
| Theoretical (1:2) | 19 | 39 |

A glance at table 7 A (page 66) shows that the 40 segregating progenies do not all give 12:3:1 ratios. Only 21 of these progenies exhibit a 12:3:1 ratio, while the other half (19 progenies) seem to approach much nearer to a 48:15:1 ratio. In order to visualize this, table 8 has been prepared. Here the data from table 7 A are arranged in two general columns, the progenies that resemble a 12:3:1 ratio being placed in one group, and those that resemble a 48:15:1 ratio in another. It is clearly seen that the total results from such a classification agree surprisingly well with the theoretical ratios.

Ratios mean very little, however, unless they are backed up by other genetic proofs. Consequently this series of ratios is nothing but a suggestion that the yellow seedling type may be really due to the action of two recessive factors, both of which are essential for the yellow color. In other words, there are duplicate determiners for the yellow seedlings, and only one of every sixteen plants in this case is yellow. The other fifteen are virescent-white, altho in some cases a very faint tinge of yellow has occurred in a virescent-white.

The $F_1$ plants that produced these 48:15:1 ratios may for the present be formulated as $L_1 l_1 L_2 l_2 V v$.

TABLE 8. $F_2$ SEEDLING PROGENIES LISTED IN TABLE 7A ARRANGED ACCORDING TO RATIOS

| Pedigree no. | Approximate ratio of 12:3:1 | | | Pedigree no. | Approximate ratio of 48:15:1 | | |
|---|---|---|---|---|---|---|---|
| 829— 9 | 220 | 39 | 25 | 829— 8 | 335 | 95 | 11 |
| | | | | —10 | 241 | 66 | 5 |
| 830— 2 | 155 | 41 | 9 | 830— 1 | 139 | 55 | 4 |
| — 5 | 54 | 15 | 4 | — 7 | 246 | 59 | 5 |
| —14 | 86 | 15 | 9 | —11 | 72 | 52 | 5 |
| —16 | 93 | 29 | 13 | —18 | 249 | 74 | 7 |
| —17 | 98 | 27 | 7 | ..... | ..... | ..... | ..... |
| —19 | 88 | 19 | 5 | ..... | ..... | ..... | ..... |
| 882— 3 | 237 | 43 | 12 | 882— 1 | 256 | 71 | 12 |
| —10 | 179 | 47 | 9 | — 2 | 203 | 77 | 4 |
| —12 | 174 | 46 | 14 | — 5 | 236 | 73 | 3 |
| —15 | 228 | 64 | 21 | — 9 | 238 | 69 | 3 |
| —17 | 216 | 66 | 18 | —13 | 200 | 62 | 9 |
| —18 | 162 | 32 | 16 | —14 | 230 | 86 | 4 |
| —20 | 132 | 40 | 13 | —21 | 169 | 65 | 3 |
| | | | | —22 | 221 | 68 | 4 |
| 883— 6 | 113 | 36 | 10 | 883— 2 | 176 | 40 | 2 |
| —19 | 143 | 37 | 15 | — 3 | 238 | 80 | 6 |
| —22 | 135 | 29 | 11 | —12 | 153 | 32 | 1 |
| —25 | 163 | 39 | 13 | —13 | 246 | 76 | 7 |
| —26a | 129 | 26 | 10 | —26 | 310 | 107 | 2 |
| —26c | 137 | 44 | 10 | ..... | ..... | ..... | ..... |
| —27 | 116 | 33 | 12 | ..... | ..... | ..... | ..... |
| Total | 3,058 | 767 | 256 | Total | 4,158 | 1,307 | 97 |
| Theoretical | 3,061 | 765 | 255 | Theoretical | 4,171 | 1,304 | 87 |
| Closeness of fit (P) for totals | $\chi^2 = 0.011$ P = Very good fit | | | | $\chi^2 = 1.260$ P = 0.545 | | |

Another source of evidence on the relation between the *L* and *V* factors is afforded by two crosses of the following type:

| | | |
|---|---|---|
| *llVV* | x | *LLvv* |
| 3861—1 | | 3858—2 |
| 3871—8 | | 3858—1 |

It will be noted that the female parents of the crosses come from families throwing the yellow type (table 1), altho they themselves were homozygous for the *V* factor and produced nothing but green seedlings when self-pollinated.

The $F_1$ of these crosses consisted of 170 normal greens. Ten plants were self-pollinated, and all gave $F_2$ progenies consisting of greens, virescent-whites, and yellows in the approximate ratio 12:3:1. The data appear in table 9:

TABLE 9. $F_2$ SEEDLING PROGENIES OF THE CROSS llVV x LLvv

| Pedigree nos. | Green seedlings | Virescent-white seedlings | Yellow seedlings |
|---|---|---|---|
| 3861—1 x 3858—2 | | | |
| 825—1 | 67 | 22 | 5 |
| —2 | 81 | 13 | 5 |
| —3 | 94 | 30 | 3 |
| —4 | 80 | 17 | 8 |
| 3871—8 x 3858—1 | | | |
| 843— 3 | 62 | 29 | 5 |
| — 7 | 93 | 19 | 10 |
| — 8 | 104 | 31 | 9 |
| —10 | 38 | 10 | 3 |
| —11 | 25 | 16 | 4 |
| —17 | 32 | 3 | 2 |
| Total | 676 | 190 | 54 |
| Theoretical (12:3:1) | 690 | 173 | 57 |
| Closeness of fit (P) for total | | | P = 0.3515 |

Still another interesting cross adds further evidence. In this case a green plant, which when selfed gave greens and yellows in the ratio 3:1, was crossed by a virescent-white, heterozygous for the *L* factor. The $F_1$ consisted of 73 greens, 21 virescent-whites, and 24 yellows. This is only a fair approximation to the theoretical 2:1:1 proportion.

When the green $F_1$ plants of this cross were self-fertilized the $F_2$ progenies were found to consist of two sorts, those that gave a 3:1 ratio and those that showed a 12:3:1 ratio. These are listed in table 10.

According to theory there should be equal numbers of the two classes in $F_2$. Actually there were ten of one class and eleven of the other, a very close approximation. The individual segregations check up very well with the theoretical. It happened that in this cross the segregation between the seedling types was unusually sharp and distinct.

TABLE 10. $F_2$ SEEDLING PROGENIES OF THE CROSS llVv x Llvv

| Pedigree no. | Green seedlings | Yellow seedlings | Pedigree no. | Green seedlings | Virescent-white seedlings | Yellow seedlings |
|---|---|---|---|---|---|---|
| 717— 3 | 155 | 43 | 717— 2 | 124 | 37 | 12 |
| — 4 | 45 | 15 | — 6 | 61 | 15 | 5 |
| — 9 | 40 | 16 | —25 | 155 | 28 | 18 |
| —13 | 82 | 29 | —31 | 33 | 8 | 2 |
| —14 | 39 | 24 | —38 | 80 | 16 | 14 |
| —22 | 46 | 15 | —39 | 155 | 51 | 14 |
| —23 | 39 | 13 | — 1 | Not selfed, but crossed with Llvv (Data in table 10A, page 67) | | |
| —32 | 58 | 19 | —18 | | | |
| —40 | 216 | 68 | —20 | | | |
| —41 | 122 | 36 | —26 | | | |
| | | | —37 | | | |
| Total | 842 | 278 | Total | 608 | 155 | 65 |
| Theoretical (3:1) | 840 | 280 | Theoretical (12:3:1) | 621 | 155 | 52 |

Dev./P.E. for total ..... 2.0/9.7 = 0.2 | Closeness of fit (P) for total ..... P = 0.177

Another cross was made in which the *L* and *V* factors are involved. The male parent was a virescent-white that had turned green. It was known to be homozygous for the *L* factor (*L L v v*). The female parent was green, and when selfed produced a progeny of 100 per cent green

TABLE 11. $F_2$ SEEDLING PROGENIES OF THE CROSS LlVV (3814-3) x LLvv (3858-7)

| Pedigree no. | Green seedlings | Virescent-white seedlings | Yellow seedlings | Pedigree no. | Green seedlings | Virescent-white seedlings |
|---|---|---|---|---|---|---|
| 803—1 | 140 | 37 | 12 | 803— 6 | 121 | 43 |
| —2 | 106 | 27 | 12 | — 8 | 107 | 34 |
| —4 | 134 | 24 | 9 | —10 | 63 | 16 |
| | | | | —18 | 136 | 37 |
| Total | 380 | 88 | 33 | Total | 427 | 130 |
| Theoretical (12:3:1) | 376 | 94 | 31 | Theoretical (3:1) | 418 | 139 |

Closeness of fit (P) for total: $\chi^2 = 0.555$, P = Very good fit | Dev./P. E. for total ..... 9.3/6.9 = 1.3

seedlings. Normally a cross of this kind would give a green $F_1$, and an $F_2$ consisting of 3 greens to 1 virescent-white. This cross did not so result, for a definite proportion of yellow seedlings appeared in $F_2$. Further study, however, proved that the female parent was really heterozygous for the *L* factor. The data in table 11 confirm this.

According to theory there should be two kinds of $F_1$ plants in equal numbers. One-half should produce 3 green seedlings to 1 virescent-white in $F_2$, while the other half should give a 12:3:1 ratio. There were four progenies of the first type and three of the second, fulfilling expectations very well.

As a final source of evidence on the inheritance of the *L* and *V* factors a series of fourteen crosses was made, in all of which the parental formula was *LlVv* x *Llvv*. Only the $F_1$ data are now available, and these are arranged in table 12:

TABLE 12. $F_1$ SEEDLINGS FROM THE CROSS LlVv x Llvv

| Pedigree nos. | Green seedlings | Virescent-white seedlings | Yellow seedlings |
|---|---|---|---|
| 717—18 x 832— 8 | 115 | 70 | 25 |
| —20 x — 8 | 107 | 93 | 26 |
| —26 x — 3 | 127 | 105 | 26 |
| —32 x 846— 2 | 17 | 14 | 7 |
| —37 x 847— 9 | 90 | 71 | 22 |
| 718—30 x 843—13 | 62 | 40 | 16 |
| 803— 3 x 846— 2 | 104 | 68 | 28 |
| 817— 7 x 837— 2 | 120 | 97 | 29 |
| 826—13 x 826—10 | 12 | 13 | 2 |
| 843—13 x —13 | 57 | 39 | 13 |
| 847— 4 x 847—14 | 28 | 13 | 4 |
| — 6 x —12 | 31 | 20 | 9 |
| —10 x —14 | 20 | 18 | 7 |
| 885— 2 x 826—10 | 22 | 12 | 5 |
| Total | 912 | 673 | 219 |
| Theoretical (4:3:1) | 902.0 | 676.5 | 225.5 |
| Closeness of fit (P) for total | | | $\chi^2 = 0.3164$, P = Very good fit |

The seedling progenies of all these crosses approach remarkably well the expected 4:3:1 ratio. It is undeniably true also that the sum total

of the fourteen progenies gives a ratio that proves the independent inheritance of the *L* and *V* factors according to the hypothesis already presented, for the closeness of fit in this case is exceptionally good, $\chi^2$ having a value of 0.3164.

As a result of these studies on the seedling inheritance of chlorophyll characters, the genetic formulae of these various types are thought to be represented as follows:

| Green | Virescent-white | Yellow | White |
|---|---|---|---|
| L V W<br>l V W | L v W | l v W | L V w<br>L v w<br>l V w<br>l v w |

From this arrangement it is seen that the *w* factor is considered as producing the pure white, or albino, condition, whether the dominant factors *L* and *V* are present or not. The factor *v* is responsible for the virescent condition in both the virescent-white and the yellow type. The *l* factor determines the yellow pigment in the yellow seedling, a type which also has the *v* factor. There are two types of greens, which phenotypically are identical; in one all three dominant factors are present, while in the second the *V* factor is apparently able to produce a full green color even when the recessive *l* factor is present. The reality of this second type of green (*l l V V W W*) was demonstrated in table 9 (page 22).

### INHERITANCE OF MATURE-PLANT TYPES

All the chlorophyll types in the category comprising mature plants begin as normal green seedlings. They develop their striking chlorophyll characteristics later in their ontogeny. The complete development of the chlorophyll type is best realized in the mature plant.

#### *Description of types*

*Golden* (Plate II).— The well-marked golden type was first discovered by Emerson about six years ago, in a commercial cornfield.

After a golden plant is a month or more old, the green color begins to disappear, gradually giving rise to a yellow-green and finally to a yellowish golden color. The first indications of the change appear in the tips of the older leaves. Then gradually the chlorophyll decomposes or disintegrates, and the yellow color extends to all the leaves and at the same time the stalk becomes yellow. When the plant is mature, not only the leaves and the stalk, but also the husks and the entire tassel, are yellowish golden, and the plant presents a striking appearance.

The physiology of these changes in the chlorophyll content is not understood. It appears as if the chlorophyll really decomposes, for the golden plant becomes less vigorous and some of the extremely yellow lower leaves die. It may be that the chlorophyll itself decomposes, leaving the xanthophyll pigment still intact. These changes may be similar to those producing yellow cotyledons in peas or yellow pods in beans.

There is some variation in the intensity of the yellow, or golden, color in this type. Some of the goldens could better be classed as light, or rather yellowish, green, but they are in the small minority in the material used for these studies. All these variations behave as a genetic unit, however, and it is more than likely that they are merely modifications of the golden factor, probably multiple allelomorphs.

In the leaves, the disappearance of the green color often produces a characteristic irregular spotted condition, which is not apparent in the stalk. This spotting is unlike that which is found on normal green plants, and is thought not to be genetic.

Under normal conditions it is possible to mature a small or a medium-sized ear of the golden type. Pollen formation is usually very abundant.

Variation in the golden type is noted also in the early seedling stage. Some of the plants are inclined to begin differentiating into the golden color very early, starting as light green seedlings. This is especially true under poor conditions of food and light. The majority, however, begin as fully green and do not change until they are six weeks or more old. Genetically these variations behave as a unit, altho some are more than mere fluctuations, being due very likely to the interaction of one or more seedling chlorophyll factors. For example, it is known that a golden which contains also the *l* factor shows in the early seedling stage as a yellowish green seedling.

GOLDEN TYPE. MAIN STALK AND LEAVES OF MATURE PLANT

GREEN-STRIPED TYPE. PART OF MATURE LEAF

JAPONICA WHITE-STRIPED TYPE. PART OF MATURE LEAF

JAPONICA YELLOW-STRIPED TYPE. PART OF MATURE LEAF

*Green-striped* (Plate III).— The green-striped type germinates into a fully green condition, and it is usually about two months before the green striping appears. From the color drawing (Plate III) it is apparent that the stripes in the leaves are longitudinal, alternating dark and light green, and that they are uniform in distribution; in other words, the entire leaf is uniformly striped and there is no marked variation among the leaves on a single plant. The darker green stripes appear to follow along the larger fibro-vascular bundles, while the intervening tissue shows the lighter green pigment.

Mature green-striped plants, altho apparently containing more green pigment than the golden type, are, on the average, smaller in height and in leaf area. It is only rarely that a mature ear is produced on green-striped plants. There is no difficulty in obtaining pollen, altho the plants are somewhat later in season than normal greens.

Green-striped plants are more inclined to wilt on hot days than are other sorts. The leaves even roll on a hot day following a heavy night rain.

The type originated in Emerson's pedigree cultures some six years ago, probably as a mutation. Emerson described this striping pattern in 1912, and Miles described it in 1915.

*Japonica* (Plates IV and V).— The japonica type is very well known, being sold by most seedsmen for ornamental planting. The leaves are longitudinally striped green, pale green, yellow, and white. Another name for this type is *variegated maize.*

The striping pattern is not nearly so uniform in japonica plants as in green-striped plants. Every leaf on the japonica plant is variable in the number and width of its stripes, and there is also considerable variation among individual plants in the amount of striping. Some show no striping on the leaves and indicate their japonica nature only by faint stripes on the husks; others are very prominently striped, fully 50 per cent or more of the tissue being white, pale green, or yellow. Between these extremes there are all gradations.

Japonica plants as a rule are more vigorous than either the golden or the green-striped type, and mature ears readily.

In the seedling stage there is absolutely no indication of the striping. It gradually appears only after the plant is six weeks or more old.

There are two general kinds of japonica plants. In one the stripes are pure white (Plate IV); in the other the stripes are pure yellow (Plate V), the color being very similar to that of the yellow seedlings. The two types are very distinct from each other. The japonica yellow-striped plants are very much rarer than the white-striped sort, and it is doubtful whether they have heretofore been described in any publication as a distinct type. In both types, besides these pure colors in the stripes there are also pale green stripes. These, however, are due to the superposition of colorless tissue over a deeper-lying green tissue (Miles, 1915). In the white-striped japonica plants, the colorless tissue which forms the white stripes is apparently devoid of chloroplasts. There is a sharp line of demarcation between the green and the white tissue.

Gernert (1912) mentions red stripes in the japonica type. Strictly speaking, this red color is merely an incidental distribution of a cell-sap (anthocyan) color in the non-green tissue of the japonica type. The japonica plant is entirely independent of this red color, for there are well-marked types with and without red stripes.

*Fine-striped.*— In the fine-striped type the stripes are very narrow, averaging 2 millimeters or less in width. They are white or pale green and run longitudinally along the leaf, tending to be more numerous toward the margin. The stripes appear not to have as definite a margin as those in the japonica type. There is some variation in the amount and distribution of the striping.

In this type the striping begins to differentiate in the late seedling stage, when the plant is three weeks or more old. At this time the newer leaves show much pure white tissue, but this eventually disappears when the leaves grow larger, leaving only the narrow stripes. The original fine-striped plants were found by Miles in a cornfield in Nebraska.

*Spotted.*— Spotted plants begin as normal green seedlings. When they are two months or more old, the spots begin to appear.

Mature plants exhibit a wide range of variation in the number, size, and character of the spots. In extremely spotted types the tissue becomes very much mottled, the spots often coalescing to form large areas of unhealthy-looking tissue. Such plants have difficulty in manufacturing food and seldom do they mature ears. The other limit of the range of variation shows very few spots, and often it is difficult to distinguish

these plants from normal green plants having a few accidental spots due to local external agents.

In general there are two forms of the spotted type. In one the spots have a definite margin and are nearly circular, with an average diameter of from 2 to 3 millimeters; in the other the spots are more or less irregular in outline and the margin is not distinct.

The spotted type has been described also by Emerson (1912).

### *Inheritance of the mature-plant types*

The golden, green-striped, and japonica types are all simple Mendelian recessives to normal green, as has been pointed out by Emerson (1912) and by Miles (1915). When these types are crossed with normal green plants, the $F_1$ progeny is green. When the green-striped and japonica types are crossed with green plants, the $F_1$ progeny cannot be distinguished from normal greens; but when some of the goldens are crossed with green, the heterozygous $F_1$ plants seem to be a trifle lighter green than normal plants.

The segregation in $F_2$ when golden and green-striped types are used, is very distinct. Self-pollinated ears of the $F_2$ recessives have bred true in all cases. Reciprocal crosses, where possible, are identical in $F_1$ and $F_2$.

*Japonica inheritance.*— The japonica type shows an interesting deviation from the others. When homozygous plants of this type are self-fertilized, the progeny is in some cases variable in the extent of the striping, and sometimes plants that look green occur. This is especially true when the parent plant is only slightly striped. The progeny from prominently striped japonica plants usually shows about 100 per cent of striped plants, altho occasionally a few non-striped plants appear. This is seen in table 13 (page 30).

The plants listed in table 13 as non-striped, while not showing any striping in the leaves, usually have very faint white streaks in the husks. In some cases these streaks are so few and so narrow that they easily escape observation. Such plants, however, have not lost the japonica factor, for when they are crossed with prominently striped japonica plants the $F_1$ plants are always japonica-striped. This would not be true if these near-green plants were really green genetically.

A large share of the variability of the japonica type has been traced to the influence of a certain aleurone factor. This factor plays a direct part

in determining the amount of striping in the leaves of the japonica plant. A discussion of this is reserved for a later section of this paper (page 53).

TABLE 13. PROGENY OF SELF-FERTILIZED JAPONICA PLANTS WITH DIFFERENT DEGREES OF STRIPING

| Pedigree no. | Degree of striping on parent plant | Progeny | |
|---|---|---|---|
| | | Japonica | Non-striped |
| 3605 | Prominently striped | 17 | 1 |
| 3611 | Prominently striped | 5 | 2 |
| 3612 | Prominently striped | 10 | 1 |
| 3615 | Prominently striped | 27 | 0 |
| 3606 | Medium-striped | 11 | 10 |
| 3616 | Medium-striped | 13 | 1 |
| 3617 | Medium-striped | 8 | 3 |
| 3613 | Slightly striped | 4 | 16 |
| 3614 | Slightly striped | 2 | 9 |
| 3594 | Slightly striped | 22 | 4 |

The relation between the two kinds of japonica striping (white and yellow) is interesting. Both types are recessive to normal green. When they are crossed, however, the $F_1$ plants are of the white-striped type. In some cases these $F_1$ plants show a faint yellowish tinge in the stripes, but when mature they really become white-striped japonicas. In $F_2$ both types of striping reappear in approximately a ratio of three white-striped to one yellow-striped, as shown in table 14:

TABLE 14. $F_2$ PLANTS FROM THE CROSS OF JAPONICA YELLOW-STRIPED X JAPONICA WHITE-STRIPED PLANTS

| Pedigree nos. | Japonica white-striped | Japonica yellow-striped | Doubtful |
|---|---|---|---|
| 268—1 | 72 | 31 | 18 |
| —2 | 81 | 31 | 33 |
| —3 | 48 | 20 | 17 |
| —1 x 187—4 | 29 | 10 | 10 |
| —2 x —3 | 30 | 5 | 17 |
| Total | 260 | 97 | 95 |
| Theoretical (3:1) | 268 | 89 | ..... |
| $\frac{\text{Dev.}}{\text{P. E.}}$ for total | | | $\frac{7.75}{5.52} = 1.4$ |

In table 14 the column headed *Doubtful* includes for the most part those plants in which the stripes were so small that their color (white or yellow) could not be accurately determined. Plants 187—4 and 187—3, appearing in this table, are merely heterozygous for the white-yellow condition, as was shown when they were self-fertilized.

The data in table 14 suggest a simple Mendelian relation between the japonica white- and the japonica yellow-striping, the former being dominant. This is substantiated in table 15, which shows the $F_1$ results when heterozygous japonica white-striped plants were crossed by japonica yellow-striped plants:

TABLE 15. $F_1$ PLANTS FROM THE CROSS OF HETEROZYGOUS JAPONICA WHITE-STRIPED X JAPONICA YELLOW-STRIPED PLANTS, AND RECIPROCAL

| Pedigree nos. | Japonica white-striped | Japonica yellow-striped | Doubtful |
|---|---|---|---|
| 268—3 x 266—5 | 23 | 33 | 22 |
| 3907—2 x —1 | 24 | 24 | 20 |
| 253—5 x 187—3 | 9 | 10 | 1 |
| —4 x —3 | 46 | 38 | 15 |
| 265—7 x 268—3 | 49 | 39 | 15 |
| Total | 151 | 144 | 73 |
| Theoretical (1:1) | 147.5 | 147.5 | ..... |

In table 15, plants 266—1, 266—5, 253—4, 253—5, and 265—7, were japonica yellow-striped. The approximation to the theoretical 1:1 ratio is close enough to warrant the statement made above, namely, that there is a single Mendelian-factor difference between these two types.

The genetic factor that determines this relation has been found to be identical with the seedling factor *L*. The data and discussion of this are taken up in a later section of this paper (page 39), which deals with the relation between seedling and mature-plant factors.

*Inheritance of fine-striping.*— The fine-striped type is another simple Mendelian recessive to normal green. Crosses between green and fine-striped plants always produce a fully green $F_1$ progeny. In $F_2$, there

are produced 75 per cent green and 25 per cent fine-striped plants, as is seen in table 16:

TABLE 16. $F_2$ PLANTS FROM THE CROSS OF GREEN x FINE-STRIPED PLANTS

| Pedigree no. | Green | Fine-striped |
|---|---|---|
| 3539—1 | 24 | 6 |
| 3563—2 | 24 | 6 |
| —3 | 28 | 8 |
| —4 | 20 | 8 |
| Total | 96 | 28 |
| Theoretical (3:1) | 93 | 31 |
| $\frac{\text{Dev.}}{\text{P. E.}}$ for total | | $\frac{3.0}{3.3} = 0.9$ |

A backcross on an $F_1$ plant from the cross shown in table 16, and its reciprocal cross, are presented in table 17:

TABLE 17. $F_1$ PLANTS FROM THE CROSS OF A GREEN PLANT HETEROZYGOUS FOR FINE-STRIPING, BY A FINE-STRIPED PLANT, AND RECIPROCAL

| Pedigree nos. | Green | Fine-striped |
|---|---|---|
| 3563—1 x 3574—9 | 23 | 24 |
| 3574—9 x 3563—1 | 37 | 38 |
| Total | 60 | 62 |
| Theoretical (1:1) | 61 | 61 |

*Inheritance of spotting.*— The investigation of the inheritance of spotting is not yet completed. More than thirty crosses have been made in which the spotting factor was concerned, but the results cannot as yet be classified into any definite system. When a normal green plant is crossed with a spotted plant, the $F_1$ plants usually are not spotted. Some of these crosses give spotted $F_1$ plants, but in no regular order, in some cases all the $F_1$ plants being spotted while in other cases only 2 or 3 per cent are of this type. It is not possible at present to say whether more than one factor pair is concerned.

*Genetic symbols for the mature-plant types*

Four of the mature-plant chlorophyll types discussed above were found to be Mendelian recessives to green. These have been assigned the following letters, or factors:

*g* — golden type
*st* — green-striped type
*j* — japonica type
*f* — fine-striped type

*Genetic interrelations between the various mature-plant types*

*Golden-green-striped.*— When the recessive golden and green-striped types were crossed, the $F_1$ plants proved to be normal green. In the $F_2$ generation four distinct types of plants were produced. Two were like the parents (one green-striped and one golden), one was like the $F_1$ hybrid (green), and one was entirely new, being a combination of the two recessive types, namely, a golden-green-striped type. A preliminary report of this cross was made by Miles (1915), and the complete data are arranged in table 18:

TABLE 18. $F_2$ PLANTS FROM THE CROSS GREEN-STRIPED (G G st st) x GOLDEN (g g St St)

| Pedigree no. | Green G St | Golden g St | Green-striped G st | Combination g st |
|---|---|---|---|---|
| 3356— 1 | 32 | 10 | 7 | 2 |
| — 4 | 115 | 31 | 37 | 12 |
| — 6 | 47 | 18 | 16 | 5 |
| — 8 | 9 | 4 | 1 | 2 |
| —10 | 2 | 3 | 1 | 1 |
| —15 | 75 | 24 | 28 | 2 |
| —18 | 118 | 27 | 38 | 6 |
| —23 | 87 | 33 | 34 | 5 |
| —26 | 41 | 7 | 8 | 4 |
| —28 | 32 | 9 | 7 | 5 |
| —29 | 105 | 37 | 34 | 9 |
| —31 | 68 | 17 | 14 | 5 |
| —32 | 42 | 11 | 13 | 1 |
| Total | 773 | 231 | 238 | 59 |
| Theoretical (9:3:3:1) | 732 | 244 | 244 | 81 |

The distribution in this table resembles a dihybrid Mendelian 9:3:3:1 ratio. The data do not fit such a ratio very closely, but the deviations

therefrom are largely explained by a physiological cause, which is the weakened condition of the last three classes due to their chlorophyll abnormality. The last class (golden-green-striped), especially, is not very vigorous and easily succumbs to poor climatic conditions. This combination type is of course the double recessive (*g g st st*) and should breed true to this character, but the plants are so weak that it has been impossible to mature an ear. Numerous $F_2$ plants have been self-fertilized, and some intercrosses have been made between the $F_2$ plants shown in table 18, and in every case the hypothesis has been confirmed. The data are arranged in table 18 A, in the appendix (page 68).

In all the data there is no suggestion of linkage, and it seems safe to assume that the factors *G* and *St* are inherited independently of each other.

*Golden-japonica.*— The recessive golden and japonica chlorophyll types have been crossed, and they exhibit a relation similar to the preceding one. A preliminary report of such a cross was made by Miles in 1915. The $F_1$ plants were all normal green. In the $F_2$ generation there was a segregation into four distinct types, two being like the parents (one golden and one japonica), one like the $F_1$ plants (green), and the fourth a new type, a combination of golden and japonica. The data from five such crosses (including reciprocal crosses) are arranged in table 19.

The $F_2$ distribution does not resemble very closely a 9:3:3:1 ratio. This is clearly due to the large deficiency in the japonica classes. As has been noted previously, the japonica-striping pattern sometimes fails to develop fully and the plants indicate their japonica nature only by very faint streaks in the husks. When the notes for table 19 were taken, this peculiarity of the japonica type was not understood and only those plants that showed striping in the leaves were placed in the japonica classes. The others were of course grouped with the green and the golden classes, and consequently these are in excess of the theoretical expectation.

Some of the golden-japonica (double recessive) plants of table 19 were self-fertilized. The progeny from five such plants consisted of 76 golden-japonica plants and 4 greens (due to stray pollination undoubtedly), showing that the double recessive (*g g j j*) really breeds true.

A large number of the $F_2$ plants of table 19 were self-fertilized and some were intercrossed. These data only confirm the results given above

and their detailed publication is scarcely warranted. Nothing in the results indicates a linkage between the *G* and *J* factors.

TABLE 19. $F_2$ PLANTS FROM THE CROSS JAPONICA x GOLDEN (3346, 3347, 3348), AND RECIPROCAL GOLDEN x JAPONICA (978, 979)

| Pedigree no. | Green GJ | Golden gJ | Japonica Gj | Combination gj |
|---|---|---|---|---|
| 3346— 1 | 78 | 20 | 17 | 5 |
| — 2 | 82 | 28 | 11 | 4 |
| — 3 | 17 | 10 | 12 | 0 |
| — 4 | 22 | 6 | 8 | 0 |
| 3347— 1 | 39 | 5 | 4 | 2 |
| — 2 | 37 | 7 | 6 | 2 |
| — 3 | 124 | 34 | 6 | 3 |
| — 4 | 131 | 39 | 12 | 7 |
| 3348— 1 | 96 | 21 | 6 | 0 |
| — 4 | 75 | 12 | 7 | 2 |
| — 8 | 106 | 39 | 13 | 6 |
| —11 | 84 | 37 | 29 | 11 |
| —12 | 35 | 4 | 1 | 0 |
| —13 | 98 | 25 | 6 | 6 |
| 978— 1 | 23 | 9 | 5 | 1 |
| — 2 | 26 | 7 | 11 | 3 |
| — 4 | 35 | 8 | 10 | 4 |
| — 9 | 6 | 7 | 4 | 1 |
| —10 | 14 | 10 | 1 | 0 |
| —13 | 17 | 2 | 3 | 2 |
| —15 | 32 | 8 | 6 | 1 |
| —18 | 12 | 6 | 4 | 1 |
| —19 | 13 | 2 | 4 | 0 |
| —20 | 10 | 6 | 2 | 0 |
| —21 | 14 | 4 | 7 | 0 |
| —22 | 19 | 7 | 4 | 0 |
| —24 | 11 | 5 | 6 | 0 |
| 979—13 | 26 | 8 | 5 | 3 |
| Total | 1,282 | 376 | 210 | 64 |
| Theoretical (9:3:3:1) | 1,087 | 362 | 362 | 121 |

*Japonica-green-striped.*— The $F_1$ progeny from crossing the two recessive types japonica and green-striped is normal green, with absolutely no trace of any striping pattern. The second generation from such self-fertilized $F_1$ plants consists of four types — green (*J St*), japonica (*j St*), green-striped (*J st*), and a combination of the two striping patterns (*j st*). The last-named plants are very weak and in no case has it been possible

to mature an ear on this japonica-green-striped type. Also they are very late, and hence have not even been used as the pollen parent in crosses.

The $F_2$ results from crossing a japonica by a green-striped plant are shown in table 20:

TABLE 20. $F_2$ PLANTS FROM THE CROSS JAPONICA x GREEN-STRIPED

| Pedigree nos. of parents | $F_1$ | $F_2$ | | | |
|---|---|---|---|---|---|
| | | Green J St | Japonica j St | Green-striped J st | Combination j st |
| 3468—28 x 3514—3 | 64 greens | | | | |
| 3934— 3 | ..... | 20 | 9 | 6 | 0 |
| — 5 | ..... | 12 | 10 | 8 | 0 |
| — 9 | ..... | 39 | 17 | 10 | 0 |
| —12 | ..... | 61 | 11 | 10 | 0 |
| —14 | ..... | 67 | 25 | 22 | 3 |
| —30 | ..... | 96 | 27 | 30 | 0 |
| —31 | ..... | 40 | 17 | 15 | 2 |
| —32 | ..... | 44 | 19 | 14 | 1 |
| —33 | ..... | 49 | 13 | 23 | 3 |
| —34 | ..... | 10 | 1 | 3 | 1 |
| —35 | ..... | 10 | 4 | 4 | 0 |
| —37 | ..... | 75 | 26 | 25 | 3 |
| Total | ..... | 523 | 179 | 170 | 13 |
| Theoretical (9:3:3:1) | ..... | 498 | 166 | 166 | 55 |

The large deficiency in the last class (combination) can be explained only by the physiological weakness of these japonica-green-striped plants. Save for this discrepancy, the distribution in table 20 suggests a 9:3:3:1 ratio. At least there is no indication of any appreciable linkage between the *J* and *St* factors.

*Japonica-fine-striped.*— The genetic difference between the two forms of striping in the japonica and the fine-striped plants is clearly seen when the two are crossed. The $F_1$ plants are perfectly normal green. There is a segregation in $F_2$ into four apparent types — normal green, japonica, fine-striped, and a combination of the two striping patterns. The distinction between the last three classes is very uncertain and in many cases it is impossible to distinguish between a slightly striped japonica and a fine-striped plant. Also, the combination of the two striping patterns produces very weak plants, many of which die very early.

A cross of a japonica by a fine-striped plant, and the reciprocal cross, are listed in table 21:

TABLE 21. $F_2$ PLANTS FROM THE CROSS JAPONICA x FINE-STRIPED (3567), AND RECIPROCAL (3568, 3572)

| Pedigree no. | Green J F | Japonica j F | Fine-striped J f | Combination j f |
|---|---|---|---|---|
| 3567— 1 | 47 | 9 | 7 | 4 |
| — 2 | 42 | 7 | 17 | 2 |
| — 3 | 40 | 5 | 16 | 6 |
| — 4 | 34 | 10 | 5 | 2 |
| — 6 | 36 | 7 | 6 | 1 |
| —11 | 30 | 0 | 3 | 0 |
| —12 | 38 | 6 | 10 | 2 |
| 3568—12 | 39 | 4 | 8 | 0 |
| 3572— 1 | 36 | 5 | 14 | 2 |
| — 2 | 44 | 1 | 10 | 0 |
| Total | 386 | 54 | 96 | 19 |
| Theoretical (9:3:3:1) | 310.5 | 103.5 | 103.5 | 34.5 |

This $F_2$ distribution suggests independent inheritance between the *J* and *F* factors, altho the data are rather uncertain because of the difficulty in classifying the various types of striping and also because of the differential viability of the types.

*Golden-fine-striped.*— One cross was made between the recessive types golden and fine-striped. There were 6 dark green, normal, $F_1$ plants. The results in $F_2$ are arranged in table 22:

TABLE 22. $F_2$ PLANTS FROM THE CROSS FINE-STRIPED x GOLDEN

| Pedigree no. | Green G F | Golden g F | Fine-striped G f | Combination g f |
|---|---|---|---|---|
| 3563—2 | 21 | 5 | 9 | 1 |
| —3 | 27 | 4 | 8 | 0 |
| —4 | 17 | 5 | 8 | 0 |
| Total | 65 | 14 | 25 | 1 |

These data are of little value because the numbers are too few. Also, the proportion of the goldens falls far below expectation. It is impossible

at present to determine whether or not the factors *G* and *F* are inherited independently.

The preceding results indicate that the normal green plant is composed of at least four mature-plant and three seedling chlorophyll factors. A factorial representation of this statement is shown in table 23:

TABLE 23. FACTORIAL COMPOSITION OF MATURE-PLANT TYPES

| Plant types | Factorial composition |
|---|---|
| Normal green | G J St F V L W |
| Golden | g J St F V L W |
| Japonica | G j St F V L W |
| Green-striped | G J st F V L W |
| Fine-striped | G J St f V L W |
| Virescent | G J St F v L W |
| Yellow | G J St F v l W |
| White | G J St F V L w |

## GENETIC INTERRELATIONS BETWEEN THE SEEDLING AND MATURE-PLANT TYPES

### *Factors V and St*

The genetic relation between some of the seedling factors and various mature-plant factors has been determined. Data have been accumulated which show that the *V* and *St* factors are independently inherited. Two crosses were made in which a green-striped plant (*st st V V*) was pollinated by a virescent-white plant that had turned green (*St St v v*).

There were 38 $F_1$ plants, all dark normal green both in the seedling and in the mature stage. Sixteen of these were self-fertilized, with the results given in table 24.

The excessive number of seedlings is due to the large number planted in the greenhouse for seedling counts only and not grown to maturity. Plant 3353—3 is not included in the total of the seedling counts, for there is obviously some radical disturbance here. It may be that the recessive seedling factor of the $F_1$ plant (*Vv*) mutated to the dominant *V* factor, for the mature-plant segregation remained intact.

From the results in table 24 it is fair to say that there is no suggestion of a linkage between the *V* and *St* factors, for the data agree well with the expectancy on a basis of independent inheritance.

TABLE 24. $F_2$ PLANTS FROM THE CROSS GREEN-STRIPED x VIRESCENT-WHITE

| Pedigree no. | Seedling count | | Mature-plant count | |
|---|---|---|---|---|
| | Green | Virescent-white | Green | Green-striped |
| 3353— 1 | 9 | 2 | 7 | 1 |
| — 2 | 97 | 27 | 32 | 4 |
| — 3 | *(151) | *(0) | 32 | 12 |
| — 4 | 131 | 31 | 20 | 9 |
| — 5 | 43 | 14 | 18 | 7 |
| — 6 | 148 | 36 | 32 | 10 |
| 3354— 3 | 137 | 71 | 20 | 3 |
| — 4 | 94 | 49 | 21 | 4 |
| —12 | 3 | 1 | 2 | 1 |
| —15 | 7 | 1 | 5 | 3 |
| —18 | 137 | 44 | 16 | 6 |
| —22 | 80 | 28 | 18 | 6 |
| —24 | 141 | 46 | 27 | 3 |
| 3815— 1 | 225 | 82 | 37 | 8 |
| — 4 | 220 | 81 | 24 | 10 |
| — 5 | 242 | 73 | 26 | 8 |
| Total | 1,714 | 586 | 337 | 95 |
| Theoretical (3:1) | 1,725 | 575 | 324 | 108 |
| $\frac{\text{Dev.}}{\text{P. E.}}$ for totals | $\frac{11.0}{14.0} = 0.8$ | | $\frac{13.0}{6.1} = 2.1$ | |

* Not included in totals. See text.

### *L factor and japonica striping*

Another interesting relation between the seedling and mature-plant factors is seen in the case of the *L* factor and japonica striping. It will be recalled that there are two sorts of japonica striping, the white and the yellow. The latter proved to be a simple recessive to the white-striped sort. It has been noted also that the yellow color in the yellow seedlings and that in the yellow stripes of the japonica type appear very much alike. Is it possible that the yellow seedling factor pair *Ll* governs the color in the stripes of the japonica plants?

The answer to this question was given when a homozygous virescent-white seedling (*LLvv*) was crossed with a homozygous japonica yellow-striped plant. Neither parent when self-fertilized produced any yellow seedlings. The $F_1$ plants from this cross, and from the reciprocal cross, were all fully green both in the seedling and in the mature stage. In $F_2$, however, a surprising result occurred, namely, the production of typical

yellow seedlings. This is shown in table 25. Since neither parent could produce the yellow seedling *per se*, it must be that the japonica yellow-striped parent brought in some seedling factor.

TABLE 25. $F_2$ SEEDLING PROGENIES OF THE CROSS VIRESCENT-WHITE X JAPONICA YELLOW-STRIPED, AND RECIPROCAL

| Pedigree no. | Green | Virescent-white | Yellow |
|---|---|---|---|
| 706— 3 x 1080—44 | | | |
| 1758—1 | 89 | 14 | 9 |
| —2 | 71 | 23 | 7 |
| 1130—21 x 706—18 | | | |
| 1202—2 | 4 | 2 | 1 |
| Total | 164 | 39 | 17 |
| Theoretical (12:3:1) | 165 | 41 | 14 |

Closeness of fit (P) for total ..... $\chi^2 = 0.747$

The factorial composition of the virescent-white parent was undoubtedly *JJLLvv*. The factors in the other parent must then have been either *jjLLVV* or *jjllVV*, both of which would produce green seedlings and japonica mature plants. But the use of the first formula could not explain the appearance of any yellow seedlings from the cross with a homozygous virescent-white type. The second formula, however, fits the case very well.

The $F_1$ formula would be *JjLlVv*. This would produce an $F_2$ seedling progeny of greens, virescent-whites, and yellows in the ratio 12:3:1, which hypothesis is justified by the data in table 25.

This experiment suggests that the factorial composition of the two japonica types of striping is as follows:

Japonica white-striped — *jjLLVV*
Japonica yellow-striped — *jjllVV*

Such a factorial relation is further substantiated by another cross. In this case a green plant, which when self-fertilized produced a 12:3:1 seedling ratio showing that it was heterozygous for *L* and *V*, was pollinated by a homozygous japonica yellow-striped plant. There were 91 $F_1$ plants

grown from this cross, all of which were normal green. Fourteen of these $F_1$ plants were self-fertilized and seedling progenies were grown in the greenhouse. According to theory there should be four different $F_1$ types as indicated by their seedling progeny. Two of the types should produce progenies of all green seedlings, one should produce a 12:3:1 ratio, while the fourth should give rise to a progeny of green and yellow seedlings in the ratio of 3:1. The data in table 26 show that this 2:1:1 ratio of types was surprisingly well adhered to, there being actually a proportion of 7:4:3. Consequently this cross gives further evidence that the *l* factor must be a component part of the japonica yellow-striped type.

TABLE 26. $F_2$ SEEDLING PROGENIES OF THE CROSS J J L l V v (3814-19) x j j l l V V (253-6)

| Pedigree no. | Progenies all green L l V V and l l V V | 12:3:1 progenies L l V v | | | 3:1 progenies l l V v | |
|---|---|---|---|---|---|---|
| 802— 1 | ..... | 167 | 84 | 12 | ..... | ..... |
| — 2 | ..... | ..... | ..... | ..... | 152 | 39 |
| — 4 | 83 | ..... | ..... | ..... | ..... | ..... |
| — 5 | 78 | ..... | ..... | ..... | ..... | ..... |
| — 6 | ..... | 114 | 29 | 16 | ..... | ..... |
| — 8 | ..... | 242 | 62 | 15 | ..... | ..... |
| — 9 | 47 | ..... | ..... | ..... | ..... | ..... |
| —10 | ..... | 114 | 35 | 12 | ..... | ..... |
| —12 | 47 | ..... | ..... | ..... | ..... | ..... |
| —16 | ..... | ..... | ..... | ..... | 31 | 5 |
| —18 | 46 | ..... | ..... | ..... | ..... | ..... |
| —19 | ..... | ..... | ..... | ..... | 203 | 56 |
| —20 | 82 | ..... | ..... | ..... | ..... | ..... |
| —21 | 37 | ..... | ..... | ..... | ..... | ..... |
| Total | 420 | 637 | 210 | 55 | 386 | 100 |
| Theoretical | 420 | 677 | 169 | 56 | 365 | 121 |
| Number of progenies | 7 | | 4 | | 3 | |
| Theoretical number (2:1:1) | 7 | | 3.5 | | 3.5 | |

### *Factors L and G*

A third interrelation between seedling and mature-plant factors has been determined, and this shows that the factors *L* and *G* are linked in inheritance. A consideration of this is given in the section on linkage.

## LINKAGE RELATIONS

### *Factors G and R*

In an earlier paper (Lindstrom, 1917) it has been shown that the factor pairs *Gg* and *Rr* are linked. The latter pair is one of the five pairs of aleurone factors (*Rr*, *Cc*, *Aa*, *Prpr*, *Ii*)[2] that are concerned in the development of color in the aleurone layer of the corn grain. Additional data have been accumulated on this linkage, covering not only the coupling but also the repulsion phase.

Four additional backcrosses showing coupling were made, and these are presented in table 28. The fifth cross in the table is from the earlier paper already mentioned (Lindstrom, 1917). The repulsion data are arranged in table 29.

The female parent in each of the crosses in table 28 was a green plant, heterozygous for both the *G* and the *R* factor. When selfed the plants produced an ear with 3 purple grains to 1 colorless. The male parent in each of these crosses was a pure golden type, which when self-fertilized gave all colorless grains. The aleurone factors of these parental plants have been tested by appropriate aleurone testers of known factorial constitution, so that the crosses can be represented as

*GgRrCCAAPrPrii* x *ggrrCcAAPrPrii.*

The $F_1$ grains from these crosses showed a 1:1 segregation of purple and colorless grains, as is seen in table 27:

TABLE 27. ALEURONE COUNTS OF THE CROSSES LISTED IN TABLE 28

| Pedigree nos. | Purple grains | Colorless grains |
|---|---|---|
| 914— 4 x 921—23 | 125 | 121 |
| 918— 6 x 920—11 | 148 | 142 |
| — 9 x — 1 | 168 | 149 |
| S19— 5 x —15 | 220 | 222 |
| 3472—11 x 3468—10 | 67 | 55 |
| Total | 728 | 689 |
| Theoretical (1:1) | 708.5 | 708.5 |
| $\frac{\text{Dev.}}{\text{P. E.}}$ for total | | $\frac{19.5}{12.7} = 1.5$ |

[2] Emerson has determined that there are three pairs of aleurone factors necessary for the production of any aleurone color. The factor pairs *Rr* and *Cc* have already been reported on; the studies on the new factor pair *Aa* have not yet been published but are in manuscript form. The designation for the purpling factor pair has been changed from *Pp* to *Prpr*.

The purple and the colorless seeds of these ears were planted separately. The $F_1$ progeny from the plantings is given in table 28:

TABLE 28. $F_1$ PLANTS FROM THE BACKCROSS GgRrCCAAPrPrii x ggrrCcAAPrPrii

| Pedigree nos. of parents | From purple seeds | | From colorless seeds | |
|---|---|---|---|---|
| | Green R G | Golden R g | Green r G | Golden r g |
| 914— 4 x 921—23 | 41 | 13 | 11 | 34 |
| 918— 6 x 920—11 | 34 | 6 | 5 | 23 |
| — 9 x — 1 | 42 | 14 | 20 | 42 |
| S19— 5 x —15 | 23 | 4 | 10 | 19 |
| 3472—11 x 3468—10 | 30 | 9 | 6 | 28 |
| Total | 170 | 46 | 52 | 146 |

It is evident that the linkage in this case is one in which the gametes *RG* and *rg* are associated and are produced nearly four times as often as the crossover gametes *Rg* and *rG*.

Altho there is some variation among the five backcrosses listed in table 28, it does not seem great enough to prevent the summation of the results. But before calculating the percentage of crossing-over, it is well to consider the other backcross showing repulsion between the factors *R* and *G*. The figures are given in table 29:

TABLE 29. $F_1$ PLANTS FROM THE BACKCROSS GgRrccAaPrPrii x ggrrCCAAPrPrii

| Pedigree nos. of parents | From purple seeds | | From colorless seeds | |
|---|---|---|---|---|
| | Green R G | Golden R g | Green r G | Golden r g |
| 883—12 x 919—6 | 29 | 81 | 86 | 18 |

An examination of the data in table 29 shows also that the non-crossover classes (*Rg* and *rG* in this case) occur nearly four times as often as the crossover classes (*RG* and *rg*)

A summation of the crossover and non-crossover classes in tables 28 and 29 gives 145 of the former and 483 of the latter. This makes 23 per cent of crossing-over between the *G* and the *R* factor.

### *Factors G and L*

A series of five crosses has established a linkage relation between the *G* and the *L* factor. The former is a factor that is concerned with chlorophyll development in the mature plant, while the latter is a seedling chlorophyll factor.

The first cross to point to a linkage of *G* and *L* was a cross of a virescent-white plant heterozygous for the *G* and *L* factors, by a typical golden plant. It is only rarely that a virescent-white seedling of this type matures an ear, but fortunately it was possible in this case. The $F_1$ plants from the cross were all green in the seedling stage, but segregated later into a 1:1 proportion of greens and goldens, there being 91 of the former and 102 of the latter.

Forty-five $F_1$ plants of both types were self-fertilized and the seedling progenies were grown in the greenhouse in large numbers. The $F_2$ seedling progenies are classified in table 30.

Theoretically there should be two sorts each in the green and the golden $F_1$ plants; one should give a seedling progeny of 3 greens to 1 virescent-white, and the other 12 greens to 3 virescent-whites to 1 yellow. These should occur in equal numbers if the factors *G* and *L* are inherited independently. It is evident from table 30 that this is not the case, for two of the sorts are represented in excess of the other two.

According to the pedigree records, the factors of the female parent, 3494—14 must be written as *Glv. gLv*, showing that it derived the dominant *G* and the recessive *l* factor from one parent and the recessive *g* and the dominant *L* factor from the other parent. This means that at gametogenesis the gametes *Gl* and *gL* will be produced in excess if there is any linkage between these two factors. According to the data in table 30 there is a linkage here. The crossover classes, *G L* and *g l*, occur only one-third as frequently as the non-crossover classes, for a total of the progenies in table 30 shows 11 of the former and 34 of the latter.

Within the seedling progenies of table 30 there was considerable deviation from the expected proportions in a few instances. For some reason the segregation between the seedling types was unusually poor in this cross, and in some cases it was very difficult to classify the material.

TABLE 30. $F_2$ SEEDLING PROGENIES OF THE CROSS GgLlvv (3494–14) x ggLLVV (3481–20)

| | Seedlings of green $F_1$ plants | | | | | Seedlings of golden $F_1$ plants | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3:1 progenies | | 12:3:1 progenies | | | 3:1 progenies | | 12:3:1 progenies | | |
| | 82 | 40 | 138 | 30 | 7 | 172 | 66 | 99 | 27 | 19 |
| | 147 | 40 | 84 | 22 | 6 | 165 | 61 | 107 | 59 | 15 |
| | 185 | 58 | 159 | 33 | 13 | 130 | 58 | 101 | 29 | 10 |
| | 141 | 53 | 163 | 48 | 16 | 74 | 33 | 55 | 22 | 7 |
| | 132 | 40 | 178 | 42 | 11 | 143 | 48 | .... | .... | ..... |
| | 180 | 50 | 170 | 45 | 13 | 71 | 22 | .... | .... | ..... |
| | 140 | 53 | 34 | 7 | 3 | 79 | 18 | .... | .... | ..... |
| | ..... | ..... | 93 | 21 | 7 | 145 | 49 | .... | .... | ..... |
| | ..... | ..... | 72 | 17 | 5 | 41 | 12 | .... | .... | ..... |
| | ..... | ..... | 210 | 50 | 10 | 110 | 38 | .... | .... | ..... |
| | ..... | ..... | 169 | 43 | 8 | 148 | 58 | .... | .... | ..... |
| | ..... | ..... | 109 | 24 | 11 | 97 | 21 | .... | .... | ..... |
| | ..... | ..... | 111 | 42 | 9 | 184 | 64 | .... | .... | ..... |
| | ..... | ..... | 108 | 28 | 8 | 87 | 46 | .... | .... | ..... |
| | ..... | ..... | 111 | 41 | 7 | 101 | 47 | .... | .... | ..... |
| | ..... | ..... | 119 | 25 | 14 | .... | .... | .... | .... | ..... |
| | ..... | ..... | 153 | 40 | 11 | .... | .... | .... | .... | ..... |
| | ..... | ..... | 121 | 27 | 9 | .... | .... | .... | .... | ..... |
| | ..... | ..... | 102 | 32 | 8 | .... | .... | .... | .... | ..... |
| Total..... | 1,007 | 334 | 2,404 | 617 | 176 | 1,747 | 641 | 362 | 137 | 51 |
| Theoretical. | 1,006 | 335 | 2,398 | 599 | 200 | 1,791 | 597 | 413 | 103 | 34 |
| Number of progenies. | 7 | | 19 | | | 15 | | 4 | | |

A second cross showing this linkage of *G* and *L* was made by pollinating a green plant heterozygous for the *G*, *L*, and *V* factors with a pure golden plant. As before, the $F_1$ plants were all green in the seedling stage but segregated later into 73 greens and 59 goldens, a rather poor approximation to a 1:1 ratio. When self-fertilized these $F_1$ plants produced seedling progenies as shown in table 31.

According to the factors involved, there should be four seedling factorial combinations from both the green and the golden $F_1$ plants, as shown in

TABLE 31. $F_2$ SEEDLING PROGENIES OF THE CROSS G g L l V v (3391–2) x g g L L V V (3470–25)

| | Seedlings of green $F_1$ plants | | | | | Seedlings of golden $F_1$ plants | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Green | 3:1 progenies | 12:3:1 progenies | | | Green | 3:1 progenies | | 12:3:1 progenies | | |
| | 87 | .... | 53 | 18 | 6 | 126 | 52 | 15 | 57 | 22 | 8 |
| | 137 | .... | 150 | 32 | 12 | 47 | 78 | 29 | ... | ... | .... |
| | 129 | .... | 84 | 33 | 13 | ..... | .... | .... | ... | ... | .... |
| | 30 | .... | 92 | 24 | 7 | ..... | .... | .... | ... | ... | .... |
| | 55 | .... | 167 | 59 | 17 | ..... | .... | .... | ... | ... | .... |
| | 67 | .... | 157 | 43 | 6 | ..... | .... | .... | ... | ... | .... |
| | 64 | .... | 48 | 13 | 4 | ..... | .... | .... | ... | ... | .... |
| | 107 | .... | ... | ... | ... | ..... | .... | .... | ... | ... | .... |
| Total..... | 676 | .... | 751 | 222 | 65 | 173 | 130 | 44 | 57 | 22 | 8 |
| Theoretical..... | 676 | .... | 778 | 195 | 65 | 173 | 131 | 43 | 65 | 16 | 6 |
| Number of progenies... | 0 | | 7 | | | ..... | 2 | | 1 | | |

table 32. Inasmuch as the four totally green seedling progenies cannot be distinguished phenotypically, they are grouped together in table 31, for they are not necessary in determining the relation between the *G* and *L* factors in this cross.

TABLE 32. FACTORIAL COMPOSITION AND $F_2$ BEHAVIOR OF $F_1$ GREEN AND GOLDEN PLANTS

| Factors of $F_1$ plants | $F_1$ type | $F_2$ seedling progeny |
|---|---|---|
| G g L L V V..... | Green..... | All green |
| G g L L V v..... | Green..... | 3 green to 1 virescent-white |
| G g L l V V..... | Green..... | All green |
| G g L l V v..... | Green..... | 12 green, 3 virescent-white, 1 yellow |
| g g L L V V..... | Golden..... | All green |
| g g L L V v..... | Golden..... | 3 green to 1 virescent-white |
| g g L l V V..... | Golden..... | All green |
| g g L l V v..... | Golden..... | 12 green, 3 virescent-white, 1 yellow |

A consideration of the other seedling progenies in table 31 shows that they are not produced in equal numbers, as would be the case were the factors *G* and *L* independently inherited. Instead of a proportion of 1:1:1:1 among these ten progenies, there is the odd proportion of 0:7:2:1.

Such a distribution can only suggest a linkage of the *G* and *L* factors in such a way that the non-crossover classes are produced in large excess over the crossover classes. The numbers are of course very small, but it is impossible to get large enough numbers when one is dealing with progenies rather than individuals. The intensity of this linkage is considered in connection with data from other crosses that follow.

A reciprocal cross of the preceding one, as far as the factors themselves are concerned, is presented in table 33. The same grouping of classes holds as is shown in table 31. Considering only those seedling progenies that show segregation, the proportion is seen to be 0:6:1:0, in other words, a complete linkage of the *G* and *L* factors in this case. But here again the numbers are too small to be considered by themselves.

TABLE 33 $F_2$ SEEDLING PROGENIES OF THE CROSS ggLLVV (3495–4) x GgLlVv (3495–1)

| | Seedlings of green $F_1$ plants | | | | | Seedlings of golden $F_1$ plants | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Green | 3:1 progenies | 12:3:1 progenies | | | Green | 3:1 progenies | | 12:3:1 progenies |
| | 120 | .... | 117 | 14 | 10 | 46 | 41 | 19 | ..... |
| | 42 | .... | 49 | 17 | 4 | .... | .... | .... | ..... |
| | 60 | .... | 34 | 12 | 5 | .... | .... | .... | ..... |
| | 178 | .... | 155 | 32 | 11 | .... | .... | .... | ..... |
| | .... | .... | 39 | 15 | 4 | .... | .... | .... | ..... |
| | .... | .... | 64 | 26 | 7 | .... | .... | .... | ..... |
| Total | 400 | .... | 458 | 116 | 41 | 46 | 41 | 19 | ..... |
| Theoretical | 400 | .... | 461 | 115 | 39 | 46 | 45 | 15 | ..... |
| Number of progenies | | 0 | 6 | | | .... | 1 | | 0 |

A fourth cross in which the linked factors were involved, was one in which a green plant heterozygous for the *G* and *L* factors was pollinated by a homozygous virescent-white that turned fully green. The $F_1$ plants were all green in this cross, but some were homozygous *GG* and some were heterozygous *Gg*, as was found when they were self-fertilized and the progeny were grown in the field. A summary of this cross is arranged in table 34. The detailed data of the seedling progenies have already been given in table 11 (page 23).

TABLE 34. SUMMARY OF $F_2$ SEEDLING PROGENIES OF THE CROSS GgL1VV (3814-3) x GGLLvv (3858-7)

| Seedlings of GG $F_1$ plants | | Seedlings of Gg $F_1$ plants | |
|---|---|---|---|
| 3:1 progenies | 12:3:1 progenies | 3:1 progenies | 12:3:1 progenies |
| 1 | 3 | 3 | 0 |

Altho the numbers are very small, there is a strong suggestion of a linkage between *G* and *L*. As in the three preceding crosses, the crossover gametes were *GL* and *gl* and the non-crossovers were *Gl* and *gL*. The proportion 1:3:3:0 from this cross is considered in connection with the other backcrosses, the summaries being arranged in table 35:

TABLE 35. SUMMARY OF FOUR CROSSES SHOWING LINKAGE BETWEEN G AND L FACTORS

| | GL | G1 | gL | g1 |
|---|---|---|---|---|
| From table 30 | 7 | 19 | 15 | 4 |
| From table 31 | 0 | 7 | 2 | 1 |
| From table 33 | 0 | 6 | 1 | 0 |
| From table 34 | 1 | 3 | 3 | 0 |
| Total | 8 | 35 | 21 | 5 |

There is evidently much variation among the four crosses as to the intensity of the linkage. In spite of this variation there is a decided uniformity in the crosses as to distribution, which warrants their being grouped together and considered as a unit. A summation of the crossover and non-crossover classes gives 13 of the former and 56 of the latter. This means a crossing-over percentage of approximately 19. In other words, the non-crossover gametes *Gl* and *gL*, in the four crosses listed in table 35, were produced more than four times as often as the crossover gametes *GL* and *gl*. No data are as yet available for showing the coupling phase of this linkage.

An interesting check on this linkage from a different angle was noted in a cross, the $F_2$ generation of which is shown in table 36. In this cross

a golden plant was pollinated by a japonica yellow-striped type. The factorial composition of the parents was *ggJJLL* x *GGjjll*. The $F_1$ plants from this cross were all perfectly green. Seventeen of these were self-fertilized, and the $F_2$ progenies are shown in the table.

TABLE 36. $F_2$ PLANTS FROM THE CROSS GOLDEN (ggJJLL) x JAPONICA YELLOW-STRIPED (GGjjll)

| Pedigree no. | Green | Golden | Japonica white-striped | Japonica yellow-striped | Golden-japonica-white | Golden-japonica-yellow |
|---|---|---|---|---|---|---|
| 978— 1 | 23 | 9 | 3 | 2 | 1 | 0 |
| — 2 | 26 | 7 | 9 | 2 | 3 | 0 |
| — 4 | 35 | 8 | 7 | 3 | 4 | 0 |
| — 9 | 6 | 7 | 3 | 1 | 1 | 0 |
| —10 | 14 | 10 | 0 | 1 | 0 | 0 |
| —13 | 17 | 2 | 3 | 0 | 2 | 0 |
| —15 | 32 | 8 | 3 | 3 | 1 | 0 |
| —18 | 12 | 6 | 3 | 1 | 1 | 0 |
| —19 | 13 | 2 | 2 | 2 | 0 | 0 |
| —20 | 10 | 6 | 2 | 0 | 0 | 0 |
| —21 | 14 | 4 | 6 | 1 | 0 | 0 |
| —22 | 19 | 7 | 4 | 0 | 0 | 0 |
| —24 | 11 | 5 | 5 | 1 | 0 | 0 |
| 979—13 | 26 | 8 | 3 | 2 | 3 | 0 |
| 796— 7 | 27 | 8 | 3 | 0 | 1 | 0 |
| — 8 | 29 | 9 | 7 | 2 | 1 | 0 |
| —10 | 23 | 4 | 2 | 3 | 0 | 0 |
| Total | 337 | 110 | 65 | 24 | 18 | 0 |
| Theoretical (G and L independent) | 311.8 | 103.9 | 77.9 | 26.0 | 26.0 | 8.7 |
| Theoretical (1:4 linkage) | 312 | 104 | 71 | 33 | 33 | 1 |

The numbers in table 36 are really too small to permit drawing a distinction between independent and linked inheritance, except in the last two columns. With independent inheritance there should be a 3:1 proportion between the golden-japonica-white-striped and the golden-japonica-yellow-striped class. Given a linkage on the basis of 20 per cent crossing-over, the proportion between these two classes should be 33:1. The actual data show 18 of the first and none of the second class. It is evident that there is a strong suggestion of linkage between the *G* and *L* factors.

*Relation between the L factor and aleurone color*

Since *G* is definitely linked with *R* and also with *L*, what relation does *R* bear to *L*? Theoretically, *L* should either be very loosely linked with *R* (about 40 per cent crossing-over) or be very closely linked with this aleurone factor (less than 4 per cent crossing-over). This of course follows from the fact that *G* and *R* show about 23 per cent, and *G* and *L* approximately 19 per cent, crossing-over.

Many data have been accumulated to show a definite relationship between the seedling chlorophyll factor *L* and aleurone color. The first evidence of this is derived from five crosses of green plants heterozygous for the *L* and *V* factors, by virescent-white plants heterozygous for the *L* factor. The $F_1$ grains from these crosses exhibited a segregation of colored and colorless aleurone. The colored grains were planted separately from the colorless ones, and the seedling counts from this planting are arranged in table 37:

TABLE 37. $F_1$ SEEDLINGS FROM THE CROSS L1V v x L1v v

| Pedigree nos. | From colored seeds | | | From colorless seeds | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|
| | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow |
| 717—37 x 847—9..... | 32 | 24 | 0 | 58 | 47 | 22 | 90 | 71 | 22 |
| —20 x 832—8..... | 29 | 37 | 0 | 78 | 56 | 26 | 107 | 93 | 26 |
| —26 x —3..... | 27 | 25 | 0 | 100 | 80 | 26 | 127 | 105 | 26 |
| —18 x —8..... | 17 | 11 | 0 | 98 | 59 | 25 | 115 | 70 | 25 |
| — 1 x 834—4..... | 15 | 9 | 0 | 77 | 45 | 18 | 92 | 54 | 18 |
| Total..... | 120 | 106 | 0 | 411 | 287 | 117 | 531 | 393 | 117 |
| Theoretical (4 : 3 : 1) | .... | ..... | .... | .... | ..... | .... | 521 | 390 | 130 |

Closeness of fit (P) for total..... P = 0.484

The chlorophyll factors in the parent plants necessitate a 4:3:1 proportion of green, virescent-white, and yellow seedlings. It will be noted that all three types were realized in the seedlings from the colorless seed but that only two types appeared in the progeny from the colored seed. A total of the seedlings from all the seed shows a very good approximation to the theoretical 4:3:1 ratio, indicating no disturbance of the chlorophyll factors.

The very evident failure of the colored seed to produce a single yellow seedling can be attributed only to some difference between the colored

and the colorless seed. This difference is due to some aleurone factor. Tests for aleurone composition show decisively that it is neither the *A*, the *Pr*, nor the *I* factor. But thus far no critical test has been made to determine whether it is the *R* or the *C* factor that is responsible. Indirect evidence points to the *R* factor, but further tests must be made to ascertain this. If *R* and *G*, and also *G* and *L*, are known to be linked, then it is of course very probable that it is the *R* factor which is concerned in these crosses. In this case it means that *RL* and *rl* are completely linked and the gametes *Rl* and *rL* are not produced. Such an assumption fits the facts of the case exceptionally well.

Besides these five crosses, eight $F_1$ plants of known genetic composition were self-fertilized and they also exhibited a linkage between the *L* factor and an aleurone factor. The aleurone composition of these plants was *RrCcAa*, as was determined by making proper aleurone tests and also by counting the segregation of colored and colorless grains on these self-fertilized ears. In table 38 the aleurone segregation of the eight plants

TABLE 38. NUMBER OF SEEDS WITH COLORED AND WITH COLORLESS ALEURONE FROM PLANTS LISTED IN TABLE 39

(Aleurone factors R r C c A a)

| Pedigree no. | Colored aleurone | Colorless aleurone |
|---|---|---|
| 829— 9 | 191 | 278 |
| 882— 3 | 153 | 202 |
| —10 | 168 | 263 |
| —12 | 221 | 281 |
| —15 | 246 | 356 |
| —17 | 296 | 387 |
| —18 | 186 | 301 |
| —20 | 185 | 266 |
| Total | 1,646 | 2,334 |
| Theoretical (27:37) | 1,679 | 2,301 |
| $\frac{\text{Dev.}}{\text{P. E.}}$ for total | | $\frac{33.0}{21.0} = 1.6$ |

is shown. All of them approximate very well the theoretical 27:37 ratio of colored to colorless grains, which is to be expected when the three aleurone factors *R*, *C*, and *A* are heterozygous.

The eight plants were heterozygous not only for the three aleurone factors but also for the *L* and *V* chlorophyll factors. Normally, then, they should produce in the seedling stage, green, virescent-white, and yellow seedlings in the ratio 12:3:1. The seedling progenies are classified in table 39:

TABLE 39. $F_2$ SEEDLINGS FROM SELF-FERTILIZED $F_1$ PLANTS OF THE COMPOSITION L l V v R r C c A a

| Pedigree no. | From colored seeds | | | From colorless seeds | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|
| | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow |
| 829— 9 | 67 | 21 | 0 | 153 | 18 | 25 | 220 | 39 | 25 |
| 882— 3 | 104 | 22 | 0 | 133 | 21 | 12 | 237 | 43 | 12 |
| —10 | 76 | 29 | 0 | 95 | 18 | 9 | 171 | 47 | 9 |
| —12 | 79 | 29 | 0 | 95 | 17 | 14 | 174 | 46 | 14 |
| —15 | 84 | 37 | 0 | 144 | 27 | 21 | 228 | 64 | 21 |
| —17 | 95 | 37 | 0 | 121 | 29 | 18 | 216 | 66 | 18 |
| —18 | 70 | 17 | 0 | 92 | 15 | 16 | 162 | 32 | 16 |
| —20 | 62 | 27 | 0 | 70 | 13 | 13 | 132 | 40 | 13 |
| Total | 637 | 219 | 0 | 903 | 158 | 128 | 1,540 | 377 | 128 |
| Theoretical (complete linkage of R and L) | 642 | 214 | 0 | 891 | 169 | 129 | 1,534 | 383 | 128 |

Closeness of fit (P) for total ..... $\begin{cases} \chi^2 = 0.117 \\ P = \text{Very good fit} \end{cases}$

Here again not a yellow seedling is found among the plants from the colored seeds, while the colorless seeds have produced a large number. A total of all the seedlings from both kinds of seeds gives a very close approximation to the theoretical 12:3:1 ratio, showing that the seedling inheritance is normal. Thus it is evident that some aleurone factor, probably *R*, is so related to the *L* factor that the gametes *R l* and *r L* are not produced in the above plants.

Another source of evidence on this relation comes from four self-fertilized plants, similar to the preceding in being heterozygous for *L* and *V* but having an unknown aleurone composition. The ears of these plants also showed a definite segregation of colored and colorless grains, which were planted separately. From these plantings the seedling progenies listed in table 40 were produced.

The same situation is found here as in table 39, no yellow seedlings being produced from colored seeds.

TABLE 40. $F_2$ SEEDLINGS FROM SELF-FERTILIZED $F_1$ PLANTS OF THE COMPOSITION L l V v

| Pedigree no. | From colored seeds | | | From colorless seeds | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|
| | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow | Green | Virescent-white | Yellow |
| 802— 1 | 53 | 17 | 0 | 93 | 23 | 11 | 146 | 40 | 11 |
| — 6 | 12 | 3 | 0 | 102 | 26 | 16 | 114 | 29 | 16 |
| — 8 | 72 | 25 | 0 | 170 | 37 | 15 | 242 | 62 | 15 |
| —10 | 26 | 14 | 0 | 88 | 21 | 12 | 114 | 35 | 12 |
| Total | 163 | 59 | 0 | 453 | 107 | 54 | 616 | 166 | 54 |
| Theoretical (12 : 3 : 1) | .... | ..... | .... | .... | ..... | .... | 627 | 157 | 52 |

Closeness of fit (P) for total ..... { $\chi^2 = 0.786$ P = Very good fit

All the data that have been presented on the relation of aleurone color to seedling inheritance can be explained by the complete linkage of *R* and *L*. It happens that the evidence for this linkage comes only from plants in which the gametes *RL* and *rl* are produced and *rL* and *Rl* are not produced. Whether *R* and *L* are one and the same factor cannot be determined until evidence is found showing that gametes of the type *Rl* and *rL* can be produced. Some indirect evidence has shown that the gametic combination *rL* is really produced, thus indicating that *R* and *L* are separate factors. This evidence is presented in the following section.

*Relation between japonica striping and the R factor for aleurone color*

Miles (1915) suggested a possible correlation between japonica striping and aleurone color. Evidence is now available to show that the *R* factor for aleurone color has a direct influence on the japonica striping. This fact became evident when two japonica plants were crossed. Both possessed colorless aleurone, but the $F_1$ grains from the cross exhibited a distinct segregation of 1 purple seed to 1 colorless. These seeds were planted separately.

The plants grown from purple seeds showed scarcely any japonica striping. The only indication of their japonica nature was a very faint streaking of white on the husks. The plants coming from colorless seeds, however, possessed the normal prominent type of japonica striping.

These $F_1$ plants were self-pollinated and intercrossed. They were also tested for their aleurone composition. In table 41 are presented the factorial tests for aleurone color:

TABLE 41. FACTORIAL COMPOSITION AND PLANT TYPES IN $F_1$ OF THE CROSS JAPONICA x JAPONICA

| | Pedigree nos. | Factorial composition | Plant type |
|---|---|---|---|
| Parents.. | 3481—28 x 3560—8 | RrccAAjj x rrCCAAjj | Japonica x japonica |
| $F_1$..... | 1188—1, —2, etc..... | RrCcAAjj..... | Non-striped |
| | 1189—1, —2, etc..... | rrCcAAjj..... | Japonica-striped |

Some of the $F_1$ plants were self-pollinated and intercrossed, and the aleurone counts are given in table 42:

TABLE 42. NUMBER OF SEEDS WITH COLORED AND WITH COLORLESS ALEURONE, FROM SELFED AND INTERCROSSED $F_1$ PLANTS OF THE CROSS JAPONICA x JAPONICA

| Pedigree nos. | Colored aleurone | Colorless aleurone | Ratio (approximate) | Dev / P. E. |
|---|---|---|---|---|
| 1188—1 selfed..... | 191 | 167 | 9:7 | 1.7 |
| —2 selfed..... | 184 | 142 | 9:7 | 0.1 |
| —3 selfed..... | 194 | 167 | 9:7 | 1.4 |
| 1189—2 selfed..... | 0 | 350 | ..... | ..... |
| —3 selfed..... | 0 | 295 | ..... | ..... |
| —4 selfed..... | 0 | 346 | ..... | ..... |
| —5 selfed..... | 0 | 310 | ..... | ..... |
| 1188—1 x 1189—2..... | 177 | 243 | 3:5 | 2.9 |
| —3 x 1189—5..... | 183 | 239 | 3:5 | 3.7 |
| 1189—2 x 1188—1..... | 186 | 269 | 3:5 | 2.2 |
| —3 x 1188—3..... | 192 | 326 | 3:5 | 0.3 |

It is evident that these aleurone ratios check very well with the expectation based on the factors previously assigned. The factors themselves have been determined by using certain aleurone testers of known composition.

When crossed with the *A* tester (*RRCCaa*), 1188—1, 1188—3, and 1189—4 gave fully colored ears, showing that the *A* factor was homozygous. When crossed with the *C* tester (*RRccAA*), 1188—2 and 1188—3 gave ears with a 1:1 ratio of colored to colorless grains, showing that *C* was heterozygous. The critical test, however, came when 1189—4 was crossed with the *R* tester (*rrCCAA*). The resulting ear was entirely colorless,

showing that 1189 lacked the *R* factor. A test for the *C* factor in 1189 is not necessary, because the intercrosses between 1188 and 1189, giving the 3:5 ratio (table 42), necessitate the presence of a heterozygous *C* factor. The $F_1$ plants of 1188, on the other hand, must have possessed the *R* factor (heterozygous) in order to produce the 9:7 ratio, as did 1188—1, 1188—2, and 1188—3.

It follows from this evidence that the only difference between the plants of 1188 and 1189 is the presence of the *R* factor in the former and the *r* factor in the latter. Consequently it must be this factor that reacts on the japonica striping. In other words, the *R* factor represses the striping, while the *r* factor allows its normal development.

Many data have been gathered in regard to this relation. They are arranged in table 43:

TABLE 43. RELATION BETWEEN THE ALEURONE FACTOR R AND JAPONICA STRIPING

| Pedigree no. | Progeny from colored seeds, degree of striping | | | Progeny from colorless seeds, degree of striping | | |
|---|---|---|---|---|---|---|
| | Prominent | Medium | Slight or none | Prominent | Medium | Slight or none |
| 3481—28 x 3560— 8 | 0 | 0 | 3 | 5 | 1 | 0 |
| 1188— 1 | 0 | 0 | 11 | 0 | 4 | 8 |
| — 2 | 0 | 0 | 2 | 0 | 3 | 3 |
| — 3 | 0 | 0 | 11 | 0 | 7 | 6 |
| 1189— 2 | 0 | 0 | 0 | 0 | 12 | 1 |
| — 3 | 0 | 0 | 0 | 0 | 13 | 3 |
| — 4 | 0 | 0 | 0 | 20 | 0 | 2 |
| — 5 | 0 | 0 | 0 | 31 | 0 | 0 |
| 1188— 1 x 1189— 2 | 0 | 0 | 71 | 21 | 40 | 6 |
| — 3 x — 5 | 0 | 0 | 27 | 0 | 21 | 5 |
| 1189— 2 x 1188— 1 | 0 | 4 | 51 | 7 | 33 | 16 |
| — 3 x — 3 | 0 | 0 | 21 | 17 | 0 | 2 |
| 1133—14 x — 3 | 0 | 0 | 24 | 24 | 0 | 0 |
| 1156— 2 x — 3 | 0 | 0 | 13 | 10 | 0 | 0 |

In this table the progeny come either from japonica plants that were self-pollinated, as 1188—1 and others, or from crosses of two japonica plants, so that normally all the resulting plants should be japonica-striped. A glance at the table shows that when the *R* factor is present (seeds colored) there is no prominent striping in the leaves whatsoever, while when the *r* factor is present (colorless seeds) there is a normal development of

striping. This phenomenon is far more apparent when the plants are growing in the field than when the data are seen on paper.

This fact explains, in a large measure, the peculiar variation of the japonica type. Genetically the type breeds absolutely true as a Mendelian recessive should, but the phenotypic expression of the striping is modified by the interaction of this *R* factor for aleurone color. It must be noted, however, that there is some variation in this type which cannot be due to the aleurone factor alone. This other sort of variation is seen when self-pollinated japonica plants with prominent striping produce, on an average, a progeny that is more prominently striped than the progeny from a parental type that is only slightly striped. For example, in table 43, plant 1189—4 showed more striping than plant 1189—3, and this was reflected in their progenies.

If the *R* factor is linked with the *L* factor, and the latter is instrumental in determining the sort of striping in the japonica type, is it possible that the inhibitory effect of the *R* factor on striping is really an effect on the *L* factor itself? It is known that the factors in the japonica white-striped plant are *jjLL* and those in the yellow-striped sort are *jjll*. If, then, *R* is completely linked with *L*, what is the allelomorph that goes with *r*? It cannot be *l*, for in that case the striping would be of the yellow sort, which none of the plants in table 43 showed. If it is not *l*, it must be *L* and the japonica-striped plants from colorless seed must possess the gametic combination *rL*. Consequently, in the linkage of *R* and *L*, where it was noted that only the combinations *RL* and *rl* had yet been found, it is possible that another combination, *rL*, was present. This suggests that *R* and *L* are not one and the same factor, but are separate and allow crossovers to occur between them. There is of course a chance that the three combinations *RL*, *rl*, and *rL* are multiple allelomorphs, and that the remaining combination *Rl*, which has not been demonstrated as yet, is never produced. It seems more reasonable, however, to suppose that a factor such as *R*, which is concerned with the production of an anthocyanic color in the corn grain, is not identical with *L*, a factor producing a yellow, plastid pigment in the leaves of the maize plant.

## DISCUSSION

The seven Mendelian recessive factors discussed in this paper are, of course, all chlorophyll abnormalities. The normal green maize plant

must then possess the dominant allelomorphs of these factors. A complete factorial statement of this situation is presented in table 44:

TABLE 44. FACTORIAL CONSTITUTION OF SEEDLING AND MATURE-PLANT TYPES

| Chlorophyll types | Chlorophyll factors |
|---|---|
| 1. Green | W V L G St J F or W V l G St J F |
| 2. White | w V L G St J F |
| 3. Virescent-white | W v L G St J F |
| 4. Yellow | W v l G St J F |
| 5. Golden | W V L g St J F or W V l g St J F |
| 6. Green-striped | W V L G st J F |
| 7. Japonica white-striped | W V L G St j F |
| 8. Japonica yellow-striped | W V l G St j F |
| 9. Fine-striped | W V L G St J f |

From this table it is seen that the *L* factor is really not essential for the development of green color. Consequently there are two kinds of green plants, one with the *L* factor and the other with the recessive allelomorph *l*. If the *l* factor produces the xanthophyll pigment, a supposition which the yellow pigment in the yellow seedlings merely suggests, then it may be possible to find a chemical or a physiological difference between the two types of greens mentioned above.

There are also two sorts of goldens. But in this case the presence of the *l* factor produces an effect in the seedling stage which is not apparent when the dominant allelomorph *L* is present. In other words, a golden of the type *g g l l* appears as a yellowish-green seedling, while a golden of the type *g g L L* is fully green in the seedling stage.

The effect of the *l* factor on the green-striped and fine-striped types is not yet known. In all the other chlorophyll types the function of this factor is patent.

According to the hypothesis, the *w* factor produces a white seedling that dies when the food material in the seed is used up, no matter what other chlorophyll factors are present. Theoretically it would be possible to have many types of white seedlings, depending on the various combinations of the other six chlorophyll factors. But it is impossible to test such theoretical genotypes, when the plants bearing them perish in the seedling stage.

It has been impossible to grow corn plants to maturity when more than two recessive factors for chlorophyll development are present. In fact a double recessive type is usually so weak that it is only with great difficulty that a mature ear is produced. This is a serious handicap in linkage problems, in which backcrosses to a double or triple recessive are so necessary.

The interrelations between the various chlorophyll factors suggest a factorial distribution based on the chromosome hypothesis of heredity. There are at least nine pairs of chromosomes in *Zea mays*. For the seven chlorophyll factors studied in this paper, certain genetic relations have been established. For a working hypothesis, these permit an assignment of the factors to certain chromosomes, as shown in table 45:

TABLE 45. PROVISIONAL ASSIGNMENT OF CHLOROPHYLL FACTORS TO CHROMOSOMES

| Chromosome | Probable location of factors | Other possible locations for factors listed below |
|---|---|---|
| I | L, G, R | W |
| II | V | J |
| III | St | W |
| IV-IX | W, J, F | ..... |

The disposition of the factors in table 45 is vouched for by the data herein presented, which have shown that:

1. Factors *L*, *G*, and *R* are linked;
2. Factors *L* and *V* are independent;
3. Factors *W* and *V* are independent;
4. Factors *G* and *St* are independent;
5. Factors *G* and *J* are probably independent;
6. Factors *J* and *St* are probably independent.

This makes it possible to determine with certainty five factors (*L*, *G*, *R*, *V*, and *St*) in three chromosomes (I, II, and III). Factors *W*, *J*, and *F* may be in any of the other chromosomes (IV to IX), but *W* may be also in Chromosome I or III, while *J* may be in Chromosome II. The *F* factor has been studied so little that it is better left unassigned.

Further tests are being made, however, and the factors *W*, *J*, and *F* will eventually be located accurately as to their relation with the other factors. Since there are more than thirty other Mendelian factors in maize, it will not be surprising to find that some of them are closely related to the factors already reported on.

The varied influence of the *R* factor for aleurone color on the chlorophyll factors is interesting. Not only is this factor linked with a seedling factor (*L*) and a mature-plant factor (*G*), but it is also directly concerned in the development of a pattern factor (japonica striping). This many-sided behavior of the *R* factor might indicate a fundamental chemical structure of such a nature that other factors are easily able to react with it. Further study will doubtless uncover other linkage relations with this factor.

In this connection the linkage relations of the *Gg* and *Ll* factor pairs are worth considering. In one sense these factors have opposite effects; that is, the *l* factor produces a plant that begins as a yellow seedling and later is able to turn greenish, while the *g* factor produces a plant that begins as a green seedling and later becomes yellowish or golden. Whether this situation is related in any way to the linkage of *R* with both these factors has not been determined, but there is a possibility that some such relation may obtain.

The discrepancy between the linkage values of *G* and *R* (23 per cent crossing-over) and of *G* and *L* (19 per cent crossing-over) is rather large. Since *R* and *L* show complete linkage — a fact established by large numbers of crosses — these values should theoretically be equal. Apparently the linkage value between *G* and *L* is the least dependable, for the numbers in this case are relatively small. It seems likely that this discrepancy is due merely to errors of random sampling, since the deviation is only 0.4 as large as the probable error $\left(\frac{\text{Dev.}}{\text{P. E.}} = \frac{3.1}{7.5} = 0.4\right)$. This calculation is based on the assumption that the 23-per-cent value for the linkage is more reliable than the 19-per-cent value. With such a small result as 0.4, the chances are very good that the discrepancy between these two linkage values is due to chance alone.

The inheritance of the various chlorophyll factors offers some interesting suggestions on the question of plastid inheritance. Botanists are still uncertain as to the mode of transmission of plastids from one generation

to the next. It is believed by some that plastids are either transferred bodily in the cytoplasm of the reproductive cells, or represented by special bodies, the mitochondria, which in turn are carried over from one generation to another in the cytoplasm or even in the nucleus. Morgan (1917:529) discusses this question of plastid inheritance, and is inclined to agree that chloroplasts "are transmitted as a rule only through the egg protoplasm."

On this phase of the problem the inheritance of the white seedlings may throw some light. Miles (1915) has shown that these white seedlings apparently contain no plastids. Whether or not mitochondria are present is unknown. Since white seedlings always come from perfectly green plants (heterozygous for *W*), it is obvious that the green plastids of the mother plant do not pass bodily over to the 25 per cent of the progeny which comprise these albino seedlings. A detailed study of these seedlings would show whether or not the mitochondria of the mother plant pass over to the progeny. It is of course possible that they do, and that some factor in the chromosomes prevents their normal development. At any rate it is evident that the plastids themselves do not form in the white seedlings from green mother plants, and, since they are inherited in a strict Mendelian fashion, there must be some chromosomal factor that governs their regular disappearance or nonformation. There is of course the possibility that the plastids were carried over but were destroyed before the young seedling germinated. In that case it is evident, however, that this destructive factor was carried in the chromosomes, since the inheritance is Mendelian.

The same is true of the other kinds of plastid colors — the yellow, the virescent-white, and the golden. These also may come from heterozygous green plants with perfectly normal plastids, but not all of the progeny possess plastids like the green parental ones, being either yellow, virescent-white, or golden instead of green, as the case may be. Since these plastid colors are inherited in a Mendelian manner, there must be some factor in the chromosomes that determines the expression of these plastids, whether they originate *de novo* or come from preceding bodies.

If the male nucleus in *Zea mays* is the only contribution from the male parent, it would be impossible for plastids to be inherited from the male parent unless they were carried in this nucleus. Inasmuch as the progeny

from reciprocal crosses is identical, there is no reason to suppose that the various types of plastid colors are carried over from one generation to the next as definite plastids in the cytoplasm.

For the reasons stated above, it seems improbable that plastid inheritance in corn is determined by any plastids or mitochondria in the protoplasm of the reproductive cells. It is unlikely also that plastids as such are transmitted from parent to progeny. If mitochondria are transmitted, their expression in the offspring is definitely determined by certain Mendelian factors that are undoubtedly located in the chromosomes. Hence plastid inheritance, in corn at least, should not be included in Morgan's summary statement (1917:534) that "'plastid' inheritance is at present the only known method of transmission of factors that does not come under Mendel's laws." In fact, among all the higher plants there remain only a very few isolated cases of plastid inheritance that are not Mendelian.

## SUMMARY

1. The inheritance of eight chlorophyll types is shown to be strictly Mendelian. All are recessive to normal green, which contains the dominant allelomorphs of seven chlorophyll factors — *W*, *V*, *L*, *G*, *St*, *J*, and *F*.

2. Three of the types exhibit their chlorophyll abnormalities in the seedling stage. These are the white, the virescent-white, and the yellow seedlings.

3. The five remaining types are manifested only in the mature plant. These are the golden, green-striped, japonica white-striped, japonica yellow-striped, and fine-striped types.

4. The factors *w* (for white seedlings) and *v* (for virescent-white seedlings) are independently inherited. A green plant heterozygous for *W* and *V* produces a 9:3:4 ratio of greens, virescent-whites, and whites, respectively. When the *w* factor is present, the seedlings are always white.

5. The factors *v* (virescent-white) and *l* (yellow) show independent inheritance. A green plant heterozygous for *V* and *L* produces a 12:3:1 ratio of green (*V L* and *V l*), virescent-white (*v L*), and yellow (*v l*) seedlings.

6. The factors *g* (golden) and *st* (green-striped) also are inherited independently. When these two types are crossed, the $F_1$ plants are normal green. In $F_2$ the ratio is 9 greens (*G St*), 3 goldens (*g St*), 3 green-striped (*G st*), and 1 golden-green-striped (*g st*).

7. Factors *g* (golden) and *j* (japonica), factors *g* and *f* (fine-striped), factors *j* and *st* (green-striped), and factors *j* and *f*, appear to be inherited independently. The $F_1$ plants in each cross of two such recessives are full green. In $F_2$, a 9:3:3:1 ratio is approached. The double recessive in each case is a combination of the two parental types.

8. Japonica white-striped is dominant to japonica yellow-striped. The factor that determines this relation is the seedling factor *L*. The former type is represented by the factors *jjLL*, and the latter by the factors *jjll*. Thus the *l* factor produces yellow color in both the seedling and the japonica types.

9. The factors *St* and *V* are shown to be inherited independently. The former is a mature-plant factor, while the latter is a seedling factor.

10. The golden factor pair *Gg* is linked with the aleurone factor pair *Rr*. The amount of crossing-over is approximately 23 per cent.

11. The *G* factor is linked also with the *L* seedling factor. Data from four backcrosses, in which the numbers are small, show 19 per cent crossing-over.

12. The seedling factor *L* is linked with an aleurone factor, probably *R*. In this case the linkage appears to be complete. Indirect evidence suggests that *R* and *L* are not one and the same factor.

13. The linkage relations suggest that one pair of chromosomes in maize contains the three factor pairs *Rr*, *Gg*, and *Ll*.

14. Japonica striping is directly influenced by the aleurone factor pair *Rr*. The presence of *R* represses the striping, while *r* allows normal development of the pattern.

15. These studies prove that plastid inheritance in maize is typically Mendelian.

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## APPENDIX

TABLE 2 A. $F_2$ SEEDLING PROGENIES OF THE CROSS W w V V x W W V v

| Pedigree nos. | W W V V All green | W W V v 3 green, 1 virescent-white | | W w V V 3 green, 1 white | | W w V v 9 green, 3 virescent-white, 4 white | | |
|---|---|---|---|---|---|---|---|---|
| 3008—3 x 3004—18 | | | | | | | | |
| 3342— 6 | 24 | ... | ... | ... | ... | ... | ... | ... |
| — 7 | ..... | 5 | 1 | ... | ... | ... | ... | ... |
| — 8 | ..... | 29 | 12 | ... | ... | ... | ... | ... |
| —18 | ..... | *1 | *1 | ... | ... | ... | ... | ... |
| —22 | 24 | ... | ... | ... | ... | ... | ... | ... |
| —23 | ..... | ... | ... | 60 | 29 | ... | ... | ... |
| —24 | ..... | ... | ... | ... | ... | 1 | 1 | 2 |
| —27 | ..... | ... | ... | 42 | 13 | ... | ... | ... |
| —28 | ..... | *1 | *1 | ... | ... | ... | ... | ... |
| —30 | ..... | ... | ... | 52 | 18 | ... | ... | ... |
| —31 | 25 | ... | ... | ... | ... | ... | ... | ... |
| —32 | 25 | ... | ... | ... | ... | ... | ... | ... |
| —34 | ..... | 17 | 8 | ... | ... | ... | ... | ... |
| —41 | 210 | ... | ... | ... | ... | ... | ... | ... |
| 3008—6 x 3004—18 | | | | | | | | |
| 3343— 1 | ..... | ... | ... | 7 | 1 | ... | ... | ... |
| — 2 | ..... | ... | ... | 41 | 14 | ... | ... | ... |
| — 5 | 100 | ... | ... | ... | ... | ... | ... | ... |
| — 7 | ..... | 95 | 27 | ... | ... | ... | ... | ... |
| — 9 | ..... | ... | ... | ... | ... | 149 | 48 | 65 |
| —10 | ..... | ... | ... | 89 | 31 | ... | ... | ... |
| —11 | ..... | ... | ... | ... | ... | 48 | 14 | 19 |
| —12 | ..... | ... | ... | 90 | 44 | ... | ... | ... |
| —13 | ..... | ... | ... | ... | ... | 3 | 1 | 1 |
| —13 a | 169 | ... | ... | ... | ... | ... | ... | ... |
| —14 | 84 | ... | ... | ... | ... | ... | ... | ... |
| —17 | ..... | 20 | 2 | ... | ... | ... | ... | ... |
| —18 | ..... | 19 | 6 | ... | ... | ... | ... | ... |
| —19 | 25 | ... | ... | ... | ... | ... | ... | ... |
| —20 | 104 | ... | ... | ... | ... | ... | ... | ... |
| —31 | ..... | ... | ... | ... | ... | 85 | 31 | 36 |
| —33 | ..... | ... | ... | 25 | 7 | ... | ... | ... |
| 3008—19 x 3005—3 | | | | | | | | |
| 3344— 1 | ..... | ... | ... | ... | ... | 7 | 6 | 5 |
| — 4 | ..... | ... | ... | ... | ... | 35 | 10 | 9 |
| — 5 | 107 | ... | ... | ... | ... | ... | ... | ... |
| — 7 | ..... | ... | ... | ... | ... | 51 | 16 | 23 |
| —10 | ..... | 98 | 37 | ... | ... | ... | ... | ... |
| —11 | 85 | ... | ... | ... | ... | ... | ... | ... |
| —12 | 165 | ... | ... | ... | ... | ... | ... | ... |
| —15 | ..... | ... | ... | ... | ... | 81 | 16 | 33 |
| —18 | ..... | 59 | 23 | ... | ... | ... | ... | ... |

* Progenies 3342—18 and —28 were not included in the summary (table 2, page 14) because they were not large enough to indicate whether they belonged in this class or in the 9:3:4 class.

TABLE 2A (*concluded*)

| Pedigree nos. | W W V V All green | W W V v 3 green, 1 virescent-white | | W w V V 3 green, 1 white | | W w V v 9 green, 3 virescent-white, 4 white | | |
|---|---|---|---|---|---|---|---|---|
| 3008—19 x 3005—3 (*continued*) | | | | | | | | |
| 3344—19 | ..... | ... | ... | 154 | 58 | ... | ... | ... |
| —26 | ..... | ... | ... | ... | ... | 76 | 6 | 21 |
| —29 | ..... | †(355) | †(37) | ... | ... | ... | ... | ... |
| —32 | 23 | ... | ... | ... | ... | ... | ... | ... |
| —33 | ..... | 41 | 11 | ... | ... | ... | ... | ... |
| —35 | ..... | ... | ... | 93 | 29 | ... | ... | ... |
| —36 | 25 | ... | ... | ... | ... | ... | ... | ... |
| —37 | 123 | ... | ... | ... | ... | ... | ... | ... |
| —40 | 19 | ... | ... | ... | ... | ... | ... | ... |
| —43 | ..... | 35 | 12 | ... | ... | ... | ... | ... |
| —45 | 25 | ... | ... | ... | ... | ... | ... | ... |
| 3008—33 x 3004—10 | | | | | | | | |
| 3345— 1 | ..... | 77 | 24 | ... | ... | ... | ... | ... |
| — 3 | ..... | ... | ... | 84 | 28 | ... | ... | ... |
| — 9 | 23 | ... | ... | ... | ... | ... | ... | ... |
| —17 | ..... | 46 | 5 | ... | ... | ... | ... | ... |
| —21 | ..... | 18 | 7 | ... | ... | ... | ... | ... |
| —22 | 115 | ... | ... | ... | ... | ... | ... | ... |
| —24 | ..... | ... | ... | 91 | 24 | ... | ... | ... |
| —30 | ..... | ... | ... | ... | ... | 27 | 8 | 16 |
| —33 | 65 | ... | ... | ... | ... | ... | ... | ... |
| —43 | ..... | ... | ... | ... | ... | 77 | 33 | 38 |
| —44 | ..... | ... | ... | 47 | 15 | ... | ... | ... |
| Total | 1,565 | 561 | 177 | 875 | 311 | 640 | 190 | 268 |
| Theoretical | 1,565 | 554 | 184 | 890 | 296 | 618 | 206 | 274 |

† Not included in totals. Obviously not a 3:1 ratio.

TABLE 7A. $F_2$ SEEDLING PROGENIES OF GREEN $F_1$ PLANTS FROM THE CROSS l l Vv x L L Vv AND RECIPROCAL

| Pedigree no. | L l V V Progenies all green | L l V v Progenies segregating into green: virescent-white: yellow | | |
|---|---|---|---|---|
| 829— 3 | 94 | ... | ... | ... |
| — 7 | 120 | ... | ... | ... |
| — 8 | ..... | 335 | 95 | 11 |
| — 9 | ..... | 220 | 39 | 25 |
| —10 | ..... | 241 | 66 | 5 |
| —12 | 116 | ... | ... | ... |
| 830— 1 | ..... | 139 | 55 | 4 |
| — 2 | ..... | 155 | 41 | 9 |
| — 4 | 74 | ... | ... | ... |
| — 5 | ..... | 54 | 15 | 4 |
| — 7 | ..... | 246 | 59 | 5 |
| — 9 | 50 | ... | ... | ... |
| —10 | 61 | ... | ... | ... |
| —11 | ..... | 72 | 52 | 5 |
| —12 | 55 | ... | ... | ... |
| —13 | 135 | ... | ... | ... |
| —14 | ..... | 86 | 15 | 9 |
| —15 | 130 | ... | ... | ... |
| —16 | ..... | 93 | 29 | 13 |
| —17 | ..... | 98 | 27 | 7 |
| — 18 | ..... | 249 | 74 | 7 |
| —19 | ..... | 88 | 19 | 5 |
| 882— 1 | ..... | 256 | 71 | 12 |
| — 2 | ..... | 203 | 77 | 4 |
| — 3 | ..... | 237 | 43 | 12 |
| — 5 | ..... | 236 | 73 | 3 |
| — 7 | 38 | ... | ... | ... |
| — 8 | 68 | ... | ... | ... |
| — 9 | ..... | 238 | 69 | 3 |
| —10 | ..... | 179 | 47 | 9 |
| —11 | 42 | ... | ... | ... |
| —12 | ..... | 174 | 46 | 14 |
| —13 | ..... | 200 | 62 | 9 |
| —14 | ..... | 230 | 86 | 4 |
| —15 | ..... | 228 | 64 | 21 |
| —16 | 55 | ... | ... | ... |
| —17 | ..... | 216 | 66 | 18 |
| —18 | ..... | 162 | 32 | 16 |
| —19 | 121 | ... | ... | ... |
| —20 | ..... | 132 | 40 | 13 |
| —21 | ..... | 169 | 65 | 3 |
| —22 | ..... | 221 | 68 | 4 |

TABLE 7A (*concluded*)

| Pedigree no. | L1VV Progenies all green | L1Vv Progenies segregating into green: virescent-white: yellow | | |
|---|---|---|---|---|
| 883— 2 | ..... | 176 | 40 | 2 |
| — 3 | ..... | 238 | 80 | 6 |
| — 6 | ..... | 113 | 36 | 10 |
| — 7 | 129 | ... | ... | ... |
| —12 | ..... | 153 | 32 | 1 |
| —13 | ..... | 246 | 76 | 7 |
| —14 | 99 | ... | ... | ... |
| —17 | 94 | ... | ... | ... |
| —19 | ..... | 143 | 37 | 15 |
| —21 | 93 | ... | ... | ... |
| —22 | ..... | 135 | 29 | 11 |
| —25 | ..... | 163 | 39 | 13 |
| —26 | ..... | 310 | 107 | 2 |
| —26a | ..... | 129 | 26 | 10 |
| —26c | ..... | 137 | 44 | 10 |
| —27 | ..... | 116 | 33 | 12 |

TABLE 10A. $F_1$ SEEDLINGS FROM THE CROSSES LISTED IN TABLE 10, L1Vv x L1vv

| Pedigree nos. | Green seedlings | Virescent-white seedlings | Yellow seedlings |
|---|---|---|---|
| 717— 1 x 832—4 | 92 | 54 | 18 |
| —18 x —8 | 115 | 70 | 25 |
| —20 x —8 | 107 | 93 | 26 |
| —26 x —3 | 127 | 105 | 26 |
| —37 x 847—9 | 90 | 71 | 22 |
| Total | 531 | 393 | 117 |
| Theoretical (4:3:1) | 521 | 390 | 130 |
| Closeness of fit (P) for total | | | P = 0.484 |

TABLE 18 A. $F_3$ PROGENIES OF SELF-POLLINATED AND INTERCROSSED $F_2$ PLANTS LISTED IN TABLE 18

(Parents, green-striped x golden)

| Pedigree no. | Progeny from green $F_2$ plants | | | | Pedigree no. | Progeny from golden $F_2$ plants | |
|---|---|---|---|---|---|---|---|
| | Green | Golden | Green-striped | Combination | | Golden | Combination |
| 3518— 2 | 21 | 8 | 8 | 3 | 3518— 4 | 40 | 11 |
| —16 | 33 | 10 | 11 | 1 | — 7 | 23 | 0 |
| —30 | 30 | 14 | 6 | 2 | —15 | 46 | 10 |
| —16 x —34 | 29 | 27 | 10 | 6 | —25 | 29 | 10 |
| —32 x — 4 | 30 | 19 | 0 | 0 | —34 | 11 | 3 |
| —30 x —25 | 3 | 6 | 2 | 3 | 3520— 1 | 37 | 12 |
| 3521— 5 | 25 | 0 | 9 | 0 | 3521— 3 | 6 | 1 |
| —17 | 17 | 4 | 8 | 1 | — 3 x —21 | 24 | 11 |
| —18 | 26 | 12 | 7 | 4 | | | |
| —28 | 32 | 0 | 1 | 0 | | | |
| —36 | 13 | 0 | 1 | 0 | | | |
| 3522—22 | 13 | 4 | 9 | 2 | 3522—10 | 13 | 0 |
| | | | | | —15 | 8 | 4 |
| 3523— 1 | 19 | 0 | 10 | 0 | 3523— 2 | 16 | 0 |
| — 9 | 10 | 9 | 8 | 3 | —17 | 21 | 0 |
| —12 | 9 | 1 | 4 | 0 | 3524—30 | 9 | 4 |
| —14 | 12 | 3 | 4 | 2 | | | |
| —12 x —17 | 7 | 8 | 0 | 0 | | | |
| — 9 x 3522–10 | 20 | 10 | 0 | 0 | | | |
| 3525— 3 | 20 | 0 | 3 | 0 | 3525—12 | 7 | 0 |
| —16 | 14 | 2 | 6 | 1 | —15 | 21 | 0 |
| —16 x —17 | 4 | 1 | 0 | 0 | —17 | 4 | 0 |
| | | | | | 3526— 9 | 24 | 0 |
| | | | | | —18 | 19 | 8 |
| | | | | | 3527— 8 | 34 | 0 |
| 3528— 2 | 28 | 4 | 5 | 5 | 3528— 6 | 3 | 0 |
| —23 | 5 | 0 | 2 | 0 | —11 | 19 | 7 |
| 3529— 1 | 23 | 13 | 0 | 0 | —26 | 14 | 4 |
| —12 | 7 | 0 | 0 | 0 | —28 | 31 | 9 |
| —23 | 4 | 1 | 1 | 0 | | | |
| — 1 x 3528–20 | 34 | 32 | 0 | 0 | | | |
| 3530— 1 | 19 | 0 | 0 | 0 | 3530— 3 | 28 | 0 |
| — 8 | 6 | 0 | 0 | 0 | | | |
| — 9 x — 8 | 38 | 0 | 0 | 0 | | | |
| —10 x — 8 | 25 | 4 | 0 | 0 | | | |

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# STIMULATION OF ROOT GROWTH IN CUTTINGS BY TREATMENT WITH CHEMICAL COMPOUNDS

OTIS F. CURTIS

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# STIMULATION OF ROOT GROWTH IN CUTTINGS BY TREATMENT WITH CHEMICAL COMPOUNDS

# STIMULATION OF ROOT GROWTH IN CUTTINGS BY TREATMENT WITH CHEMICAL COMPOUNDS[1]

Otis F. Curtis

Increasing numbers of plants must of necessity be propagated vegetatively, either because of the difficulties involved in propagation by seed or because many valuable forms do not reproduce true to seed. A large proportion of such plants are started as cuttings, which when placed under suitable conditions will develop into complete plants. In spite of the very general use and importance of this method of propagation, no adequate investigations have thus far been made concerning the principles or the factors involved.

When the importance of propagating plants by cuttings is considered, the value of any treatment that will stimulate root formation in cuttings is obvious. Many special methods of treatment have been suggested. For the most part these are based on practical experience, yet the reasons given for the practices described are often directly conflicting or are not well founded on physiological facts so far as these are known. It would seem, therefore, that some definitely directed research in the physiology of root formation in cuttings would be of value in this field.

During some investigations to determine the effect of various chemical compounds on the rest period of woody plants, conducted in the Laboratory of Plant Physiology at Cornell University, it was found that when twigs of *Ligustrum ovalifolium* Hassk. were treated for a short time with a solution of potassium permanganate, roots developed to a greater extent than on the checks or on twigs treated with other compounds. These results suggested the possibility of an investigation concerning the effect of various chemical compounds on the root growth of cuttings, and this has been the primary purpose of the present investigation. No experiments have been conducted to compare directly the value of different methods in common practice among propagators, as those methods cover

[1] Contribution from the Laboratory of Plant Physiology, Cornell University.

chiefly the moisture, temperature, and light relations, as well as the effect of the time and manner of making the cuttings. Some of those practices, however, have been briefly discussed in the latter part of this paper, in so far as they are related to the present investigation.

In the experiments conducted by the writer, the cuttings, taken under different conditions as stated for each experiment, were subjected either to a limited or to a continuous treatment with the various compounds used. For limited treatment the time ranged for the most part from one to two days. The cuttings were then rinsed and placed in flasks or in sand. For continuous treatment the cuttings were placed in flasks containing the various compounds dissolved in distilled water, tap water, or full nutrient solution. A few tests were made in which the compounds were applied to sand in pots or flats and the cuttings were placed directly in these, but no very decided results have thus far been obtained.

For the limited treatments 100 cubic centimeters of solution was used unless otherwise stated. These treatments were administered either in tall glass cylinders, in large test tubes, in flasks, or in tumblers. The cuttings that were left in liquid media were placed in Erlenmeyer flasks of resistance glass, 250 cubic centimeters in capacity. The flasks were carefully cleaned and then covered with black paper. In the majority of cases ten twigs were placed in each container, and the containers were set in trays on benches in the greenhouse. No special precautions were taken for controlling the temperature and the relative humidity. The cuttings in sand were on a greenhouse bench with no bottom heat.

In comparing the relative values of the several treatments, the average total root length per twig was taken as the best criterion. The number of roots and the average length of the individual roots were also determined in some cases, but these figures were not consistent. For example, in a given culture one twig might have a large number of short roots while another had a small number of long roots, and therefore, according to the number of roots, the two would be quite distinctive. The total root length per twig, however, proved to be fairly constant. The total green and dry weights per culture were determined in a few instances.

In choosing a form with which to experiment, there were several points that had to be considered, as follows:

1. Large numbers of cuttings must be available.

2. The cuttings must be uniform with respect to size, shape, age, position on parent form from which they were taken, and conditions under which they were grown. Otherwise they would be likely to root unevenly.

3. Uniformity in rooting was a very important factor, for without uniformity there was found to be a large probable error which would necessitate the using of great numbers of twigs for each treatment, thereby complicating and increasing the mechanical labor involved. In view of the fact that in these experiments over twelve thousand cuttings of Ligustrum were actually used in addition to four thousand cuttings of other species, it is obvious that the problem would be rendered more difficult if it were necessary to increase the number of cuttings as much as five to ten times.

4. It was important that cuttings should be used which would root in as short a time as possible. The field of research is new, and if one were forced to wait two months or more for results on preliminary tests the experiments would be long drawn out or it would be too late to obtain cuttings for a second set. The writer experienced this trouble for three consecutive years, even with comparatively quick-rooting Ligustrum. On those occasions the December freezes had killed the twigs on the bushes at about the time when the first set of cuttings was showing results. Furthermore, the immature condition of the twigs rendered impossible an earlier beginning of the preliminary experiments. The use of hardy forms would not solve this difficulty, for, tho freezing would not kill the twigs, it would bring them out of the resting condition, which would be detrimental to rooting.

5. It was necessary to choose a form that would root readily. Comparative results could thus be obtained which would allow for manipulation to determine more nearly the optimum treatment.

*Ligustrum ovalifolium* Hassk. most nearly fitted the requirements outlined, and therefore it was used in the majority of the experiments. The following forms also were used: *Cydonia oblonga* Mill., *Ribes Houghtonianum* Janez., *Pyrus malus* Linn., *Prunus cerasifera* Ehrh., *Kerria japonica* DC., *Evonymus europaea* Linn., *Berberis Thunbergii* DC.,

*Diervilla* sp., *Populus nigra* var. *italica* Du Roi, *Spiraea Vanhouttei* Zabel, *Forsythia* sp., three species of Salix, *Iresine Herbstii* Hook. f., and *Lycopersicum esculentum* Mill.

## PART I. EFFECT OF INORGANIC COMPOUNDS ON ROOT GROWTH

### EFFECT OF NUTRIENT SOLUTIONS

In order to be able to follow more closely the development of the roots, it was necessary to grow the cuttings in liquid media. To determine whether a nutrient solution might increase root growth, various strengths of Knop's and Crone's solutions were employed, as indicated in table 1. Cuttings of *Ligustrum ovalifolium* were taken from two hedges which had been growing under somewhat different conditions. The twigs from one hedge (Column B in table 1) soon produced a strong growth of tops, resulting in such a large increase in transpiration surface and

TABLE 1. EFFECT OF NUTRIENT SOLUTIONS ON ROOT GROWTH IN WOODY CUTTINGS

(Continuous treatment from November 21, 1914, to January 8, 1915. Ten twigs to a culture)

| Solution | A | | B |
|---|---|---|---|
| | Average total length of roots per twig (millimeters) | Number of twigs rooted | Number of twigs rooted |
| Crone's solution,* 0.5 per cent | ..... | ..... | Dead |
| 0.1 per cent | ..... | ..... | Dead |
| 0.01 per cent | ..... | ..... | 5 |
| Knop's solution,† 0.5 per cent | Dead | 0 | Dead |
| 0.1 per cent | 110±26.4 | 6 | Dead |
| 0.01 per cent | 251±23.8 | 10 | 4 |
| Modified Knop's solution, ‡0.5 per cent | Dead | 0 | Dead |
| 0.1 per cent | 72±27.5 | 7 | Dead |
| 0.01 per cent | 260±28.5 | 10 | 3 |
| Tap water | 218±26.8 | 10 | 3 |
| Distilled water | 203±37.5 | 10 | ..... |

* Crone's solution contained salts in the following proportions: $KNO_3$, 4; $CaSO_4$, 2; $MgSO_4$, 2; $Fe_2(PO_4)_2$, 1; $Ca_3(PO_4)_2$, 1.

† Knop's solution contained salts in the following proportions: $Ca(NO_3)_2$, 1; $KNO_3$, 0.25; $MgSO_4$, 0.25; $KH_2PO_4$, 0.25; $Fe_2(PO_4)_2$, 0.05.

‡ The modified Knop's solution was similar to the preceding but contained five times the proportion of iron phosphate. In both cases iron phosphate was used in place of iron chloride.

in loss of water that the flasks containing them became dry. The twigs in some of the cultures had produced roots. Such cases were noted but no measurements were taken. The twigs from the other hedge (Column A in the table) remained dormant for some time and the buds were just starting at the time when the roots were measured.

It is shown fairly clearly in table 1 that nutrient solutions of the strengths used in culture work with seedlings are distinctly injurious to woody cuttings. This injurious effect of nutrient solutions, especially at the higher concentrations — 0.1 per cent or above — was further proved by subsequent experiments in which similar results were obtained. In four experiments, sixteen out of a total of twenty cultures showed distinct retardation of growth on the addition of nutrient solutions. Even single nutrient salts, such as $CaCl_2$, $NaH_2PO_4$, $KNO_3$, and $KH_2PO_4$, in very dilute solutions, showed marked retardation of the root growth. No very extensive experiments with nutrient solutions were attempted, since the few results obtained showed clearly that such treatments tend to be more injurious than beneficial to woody cuttings. A few experiments with herbaceous cuttings indicated that these are less injured by concentrations up to 0.2 per cent than are woody forms.

The root development in woody cuttings is usually lessened by an increase in concentration of the nutrient solution, as shown by the figures in table 1. This is somewhat comparable to the effect of high concentrations of soil or nutrient solutions on seedlings observed by a number of investigators — Polle (1910), Harris (1914), Stiles (1915), Brenchley (1916), and many others. The writer has found, however, that woody cuttings are much less tolerant of the stronger concentrations than are seedlings.

A discussion of the causes for increase or decrease of root growth resulting from a change in concentration of nutrient solutions, and reports of further experiments, are reserved for a later paper.

### INFLUENCE OF TREATMENT WITH POTASSIUM PERMANGANATE

As already stated, it was found that twigs of *Ligustrum ovalifolium* developed more extensive roots when treated with potassium permanganate than when treated with a number of other compounds. Potassium permanganate was therefore tried in the first of these experiments. In

order to determine the limiting concentrations, as well as the optimum time of treatment, single lots of ten cuttings each of *Ligustrum ovalifolium* were treated as indicated in table 2:

TABLE 2. INFLUENCE OF CONCENTRATIONS AND OF DURATION OF TREATMENT WITH $KMnO_4$ ON CUTTINGS OF LIGUSTRUM OVALIFOLIUM

(Cuttings taken on November 29, 1913)

| Solutions used and time of treatment | Cuttings grown in solutions in flasks, or treated and placed in tap water. Roots measured January 14, 1914 | | | |
|---|---|---|---|---|
| | Average total length of roots per twig (millimeters) | Average total length of roots relative to check as unity | Average number of roots to the twig | Average length per root (millimeters) |
| Check | 88.4±18.7 | 1.00±0.21 | 8.8 | 10.0 |
| Treatment 24 hours | | | | |
| $KMnO_4$, 2 per cent | 361.4±31.9 | 4.09±0.36 | 15.2 | 23.8 |
| 1 per cent | 317.0±15.0 | 3.59±0.17 | 13.9 | 22.8 |
| 0.5 per cent | 276.0±36.5 | 3.12±0.41 | 10.8 | 25.6 |
| Treatment 5 days | | | | |
| $KMnO_4$, 0.50 per cent | 234.0±31.2 | 2.65±0.35 | 9.6 | 24.3 |
| 0.25 per cent | 217.0±30.6 | 2.45±0.35 | 11.8 | 18.5 |
| 0.10 per cent | 60.0±11.0 | 0.68±0.12 | 4.3 | 14.2 |
| 0.05 per cent | 26.0±13.9 | 0.29±0.16 | 3.2 | 7.9 |
| Continuous treatment | | | | |
| $KMnO_4$, 0.10 per cent | 294.0±25.0 | 3.33±0.28 | 12.6 | 23.4 |
| 0.05 per cent | 183.0±14.8 | 2.07±0.17 | 13.3 | 13.8 |
| 0.01 per cent | 145.0±14.5 | 1.64±0.17 | 9.1 | 15.8 |
| 0.005 per cent | 176.0±16.6 | 1.99±0.19 | 10.2 | 17.1 |
| 0.001 per cent | 115.0±21.3 | 1.30±0.24 | 8.5 | 13.5 |
| 0.0001 per cent | 44.0±11.5 | 0.50±0.13 | 4.1 | 10.8 |

TABLE 2 (*concluded*)

| Solutions used and time of treatment | Cuttings treated and placed in sand. Roots measured January 19, 1914 | | | |
|---|---|---|---|---|
| | Average total length of roots per twig (millimeters) | Average total length of roots relative to check as unity | Average number of roots to the twig | Average length per root (millimeters) |
| Check | 149.0 | ..... | 13.0 | 11.4 |
| Check | 143.0 | ..... | 11.2 | 12.8 |
| Average of checks | 146.0±12.1 | 1.00±0.08 | 12.1 | 12.1 |
| Treatment 24 hours | | | | |
| $KMnO_4$, 2 per cent | 183.0±18.5 | 1.25±0.13 | 9.8 | 18.2 |
| 1 per cent | 352.0±15.0 | 2.41±0.10 | 17.3 | 20.4 |
| 0.5 per cent | 211.0± 7.2 | 1.45±0.05 | 14.0 | 15.0 |
| Treatment 5 days | | | | |
| $KMnO_4$, 0.50 per cent | 287.0±20.6 | 1.97±0.14 | 11.4 | 25.2 |
| 0.25 per cent | 212.0± 6.6 | 1.45±0.05 | 10.6 | 20.0 |
| 0.10 per cent | 199.0±22.1 | 1.36±0.15 | 12.0 | 16.6 |
| 0.05 per cent | 111.0±12.5 | 0.76±0.08 | 8.0 | 15.3 |

As shown by table 2 and also by figure 1, potassium permanganate causes a marked stimulation of root growth in Ligustrum in the 24-hours, 5-days, and continuous treatments. With but one exception the maximum stimulation occurred in the strongest solutions, indicating that higher concentrations might give even better results. Subsequent experiments have shown, however, that concentrations close to the optimum were used in the 24-hours and continuous treatments. The optima in these two gave results of 4.09±0.36 and 3.33±0.28, respectively, relative to the check as unity. The difference between the check and the best treatment is over eight and a half times the probable error. The cuttings placed in the sand, as shown by the same table, indicated a lesser degree

of stimulation, but the optimum results show a root growth $2.41 \pm 0.10$ and $1.97 \pm 0.14$ times that of the control. Tho but single cultures were used, and there were only five twigs in the sand cultures — except in the check, in which the number was sixteen — yet the results were unexpectedly consistent, showing a continuous change with change in concentration with one unimportant exception in which the culture having a slight increase in concentration had a somewhat lower root length. In four cases the weakest concentrations gave a root length shorter than

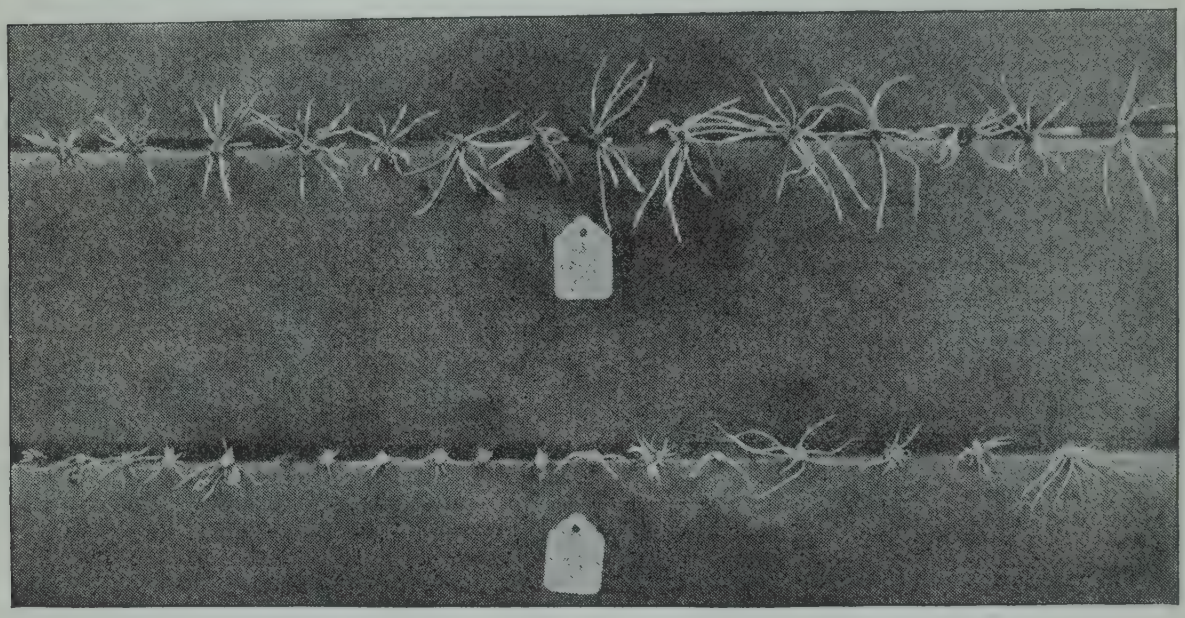

FIG. 1. LIGUSTRUM CUTTINGS AS AFFECTED BY TREATMENT WITH POTASSIUM PERMANGANATE

Upper row: Cuttings treated for twenty-four hours in 1-per-cent $KMnO_4$; the five at the left then placed in sand, the remainder in tap water

Lower row: Check. Cuttings left for twenty-four hours in tap water; the five at the left then placed in sand, the remainder in tap water

that in the check. These dilutions were so great and the results so similar to those of the check that the latter may indicate merely a probable variation between separate checks.

The stimulation here obtained has been fully confirmed by later experiments in which duplicate and triplicate cultures were made, and by others in which one hundred or more twigs were used in each treatment. This table was given in preference to the others, as the single experiment covers a wider range of concentrations and lengths of treatment than any one subsequent experiment.

In addition to the experiment just reported, Ligustrum was used in nine other experiments in which the cuttings were treated with potassium permanganate. In these experiments, some of which are described later in this paper, there were fifty-two treatments with potassium permanganate at different concentrations, usually in duplicate, and for different lengths of time. All these fifty-two treatments, with the exception of three in which the concentrations were too high, showed stimulation of root growth above that obtained in the checks.

Since Ligustrum was so clearly benefited by the treatment, a few experiments were made to determine whether or not other species would be similarly affected. Some of these experiments were started in the latter part of winter, which proved to be too late for successful rooting. Cuttings of Ribes, Cydonia, and Berberis formed roots and the results seemed to indicate some stimulation, but there was such wide variation between duplicate cultures that no definite conclusions could be drawn.

Treatment with potassium permanganate stimulated root growth in cuttings of a number of woody plants, as is shown in table 3. With several forms the treatment not only resulted in an increase in root length per twig, but also caused a larger proportion of cuttings to take root. The results obtained with *Prunus cerasifera* are shown in figures 2 and 3.

All the forms here reported can be fairly readily propagated by hardwood cuttings if these are taken at the proper time of year and if sufficient precautions are used in setting and handling them. It is apparent, however, that if the cuttings are taken late in the season and placed in the sand, with no especial precautions regarding the supply of bottom heat, moisture, light, and temperature, a treatment with potassium permanganate results in a marked improvement in root production in respect both to the aggregate length and dry weight of the roots of a given twig and to the proportion of twigs forming roots. In addition to the experiments reported in table 3, an experiment with Ligustrum shows very clearly this improvement under adverse conditions. Cuttings were taken very late in the season — March 16, 1917. Contrary to the usual practice, the base of each twig was cut square across with rather dull pruning shears and no clean diagonal cut was made with a sharp knife. The twigs were treated as indicated in table 4 and then placed in sand. Because of the lateness of the season and the rather careless treatment, the check twigs failed to develop roots as freely as

TABLE 3. EFFECT OF $KMnO_4$ ON CUTTINGS OF KERRIA JAPONICA, PRUNUS CERASIFERA, DIERVILLA SP., POPULUS NIGRA VAR. ITALICA, EVONYMUS EUROPAEA, FORSYTHIA SP., SPIRAEA VANHOUTTEI

| Plant | Number of twigs per culture | Solution (molecular concentration) | Duration of treatment | Date when cuttings were taken | Date when records were made | Roots | | | Tops | | Number of twigs rooted | Twigs with no roots but calloused | Twigs living but with no roots and no calli | Twigs dead either at base or thruout |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Average length per twig (millimeters) | Average dry weight per twig (grams) | Average length or dry weight relative to check as unity | Average length per twig (millimeters) | Average dry weight per twig (grams) | | | | |
| Prunus... | 9 | Distilled water. | Continuous..... | 9/17/1915 | 10/23/1915 | 2.4± 0.9 | ..... | 1.00±0.37 | ... | ..... | 4 | 1 | 2 | 2 |
| Prunus... | 10 | 0.005 $KMnO_4$.. | Continuous..... | 9/17/1915 | 10/23/1915 | 92.0± 12.5 | ..... | 38.33±5.2 | ... | ..... | 10 | ... | ... | 0 |
| Prunus... | 10 | 0.001 $KMnO_4$.. | Continuous..... | 9/17/1915 | 10/23/1915 | 146.0± 22.2 | ..... | 60.83± 9.2 | ... | ..... | 9 | ... | ... | 0 |
| Kerria... | 23 | Distilled water. | 24 hours, then sand. | 12/29/1915 | 3/ 6/1916 | 27.0 | ..... | ..... | ... | ..... | 3 | 8 | 3 | 9 |
| Kerria... | 20 | Distilled water. | 24 hours, then sand. | 12/29/1915 | 3/ 6/1916 | 39.0 | ..... | ..... | ... | ..... | 3 | 8 | 0 | 9 |
| Average of checks..... | | | | ..... | ..... | 33.0± 11.5 | ..... | 1.00±0.35 | 16 | ..... | .... | ... | ... | .... |
| Kerria... | 20 | 0.1 $KMnO_4$.... | 24 hours, then sand. | 12/29/1915 | 3/ 6/1916 | 64.0± 18.8 | ..... | 1.94±0.57 | 30 | ..... | 5 | 3 | ... | 12 |
| Kerria... | 33 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 6/22/1917 | ..... | 0.00515 | 1.00 | ... | ..... | 39% | ... | ... | 61% |
| Kerria... | 27 | 0.02 $KMnO_4$... | 24 hours, then sand. | 4/ 5/1917 | 6/22/1917 | ..... | 0.02111 | 4.10 | ... | ..... | 74% | ... | ... | 26% |
| Diervilla. | 10 | Distilled water. | 24 hours, then sand. | 12/29/1915 | 3/ 6/1916 | 37.0± 13.7 | ..... | 1.00±0.31 | 53 | ..... | 6 | 3 | ... | 1 |
| Diervilla. | 10 | 0.1 $KMnO_4$ ... | 24 hours, then sand. | 12/29/1915 | 3/ 6/1916 | 535.0±100.6 | ..... | 14.46±2.72 | 63 | ..... | 9 | 0 | ... | 1 |
| Diervilla. | 19 | Tap water..... | 24 hours, then tap water | 4/ 5/1917 | 6/ 3/1917 | 115.0 | 0.0026 | 1.00 | ... | 0.080 | .... | ... | ... | .... |
| Diervilla. | 20 | 0.2 $KMnO_4$ | 24 hours, then tap water | 4/ 5/1917 | 6/ 3/1917 | 68.0 | 0.0015 | 0.59 | ... | 0.085 | .... | ... | ... | .... |
| Diervilla. | 19 | 0.1 $KMnO_4$ .. | 24 hours, then tap water | 4/ 5/1917 | 6/ 3/1917 | 181.0 | 0.0039 | 1.57 | ... | 0.082 | .... | ... | ... | .... |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Diervilla. | 20 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 6/10/1917 | ..... | 0.0035 | 1.00 | ... | ..... | 13 | 7 | ... | 0 |
| Diervilla. | 20 | 0.2 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/10/1917 | ..... | 0.0010 | 0.29 | ... | ..... | 9 | 3 | ... | 8 |
| Diervilla. | 20 | 0.1 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/10/1917 | ..... | 0.0050 | 1.43 | ... | ..... | 17 | 3 | ... | 0 |
| Diervilla. | 20 | 0.02 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/10/1917 | ..... | 0.0050 | 1.43 | ... | ..... | 13 | 6 | ... | 1 |
| Populus.. | 20 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 5/10/1917 | 25.5± 3.4 | ..... | 1.00 ±0.13 | ... | 0.060 | 14 | ... | ... | 6 |
| Populus.. | 20 | 0.1 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 5/10/1917 | 33.3± 5.0 | ..... | 1.31 ±0.20 | ... | 0.080 | 17 | ... | ... | 3 |
| Populus.. | 20 | 0.02 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 5/10/1917 | 54.0± 5.6 | ..... | 2.12 ±0.22 | ... | 0.082 | 17 | ... | ... | 3 |
| Forsythia. | 20 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | 102.0± 14.5 | ..... | 1.00 ±0.14 | ... | ..... | 13 | 2 | ... | 5 |
| Forsythia. | 21 | 0.1 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | 162.0± 22.4 | ..... | 1.59 ±0.22 | ... | ..... | 12 | 0 | ... | 9 |
| Forsythia. | 22 | 0.02 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | 269.0± 25.7 | ..... | 2.64 ±0.25 | ... | ..... | 18 | 2 | ... | 2 |
| Spiraea .. | 21 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | ..... | 0.0017 | 1.00 | ... | ..... | 10 | 4 | 0 | 7 |
| Spiraea .. | 21 | 0.2 KMnO4.. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | ..... | 0.0052 | 3.06 | ... | ..... | 10 | 0 | 6 | 5 |
| Spiraea .. | 21 | 0.1 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | ..... | 0.0043 | 2.53 | ... | ..... | 9 | 10 | 0 | 2 |
| Spiraea .. | 21 | 0.02 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | ..... | 0.0095 | 5.59 | ... | ..... | 17 | 2 | 0 | 2 |
| Evonymus | 14 | Tap water..... | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | | | | ... | ..... | 0 | 0 | 2 | 12 |
| Evonymus | 14 | 0.1 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | No measurements taken | | | ... | ..... | 0 | 0 | 1 | 13 |
| Evonymus | 14 | 0.02 $KMnO_4$ .. | 24 hours, then sand. | 4/ 5/1917 | 6/18/1917 | | | | ... | ..... | 4 | 3 | 0 | 7 |

FIG. 2. CUTTINGS OF PRUNUS CERASIFERA AS AFFECTED BY TREATMENT WITH POTASSIUM PERMANGANATE

The twigs at the left of the rule were kept continuously in 0.001 mol. $KMnO_4$; those at the right were kept continuously in water

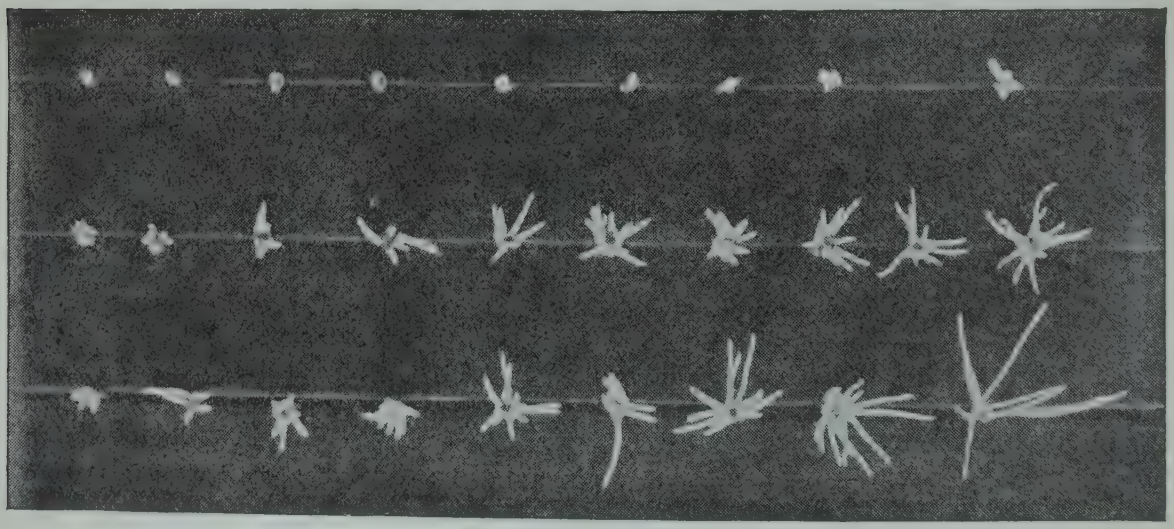

FIG. 3. CUTTINGS OF PRUNUS CERASIFERA AS AFFECTED BY TREATMENT WITH POTASSIUM PERMANGANATE

Top row: Check. Twigs from flasks containing water alone
Middle row: Twigs from flasks containing 0.005 mol. $KMnO_4$
Bottom row: Twigs from flasks containing 0.001 mol. $KMnO_4$

Ligustrum normally does. The treatment with potassium permanganate, however, largely nullified the unfavorable conditions, and both the root growth and the top development were very much increased (fig. 4).

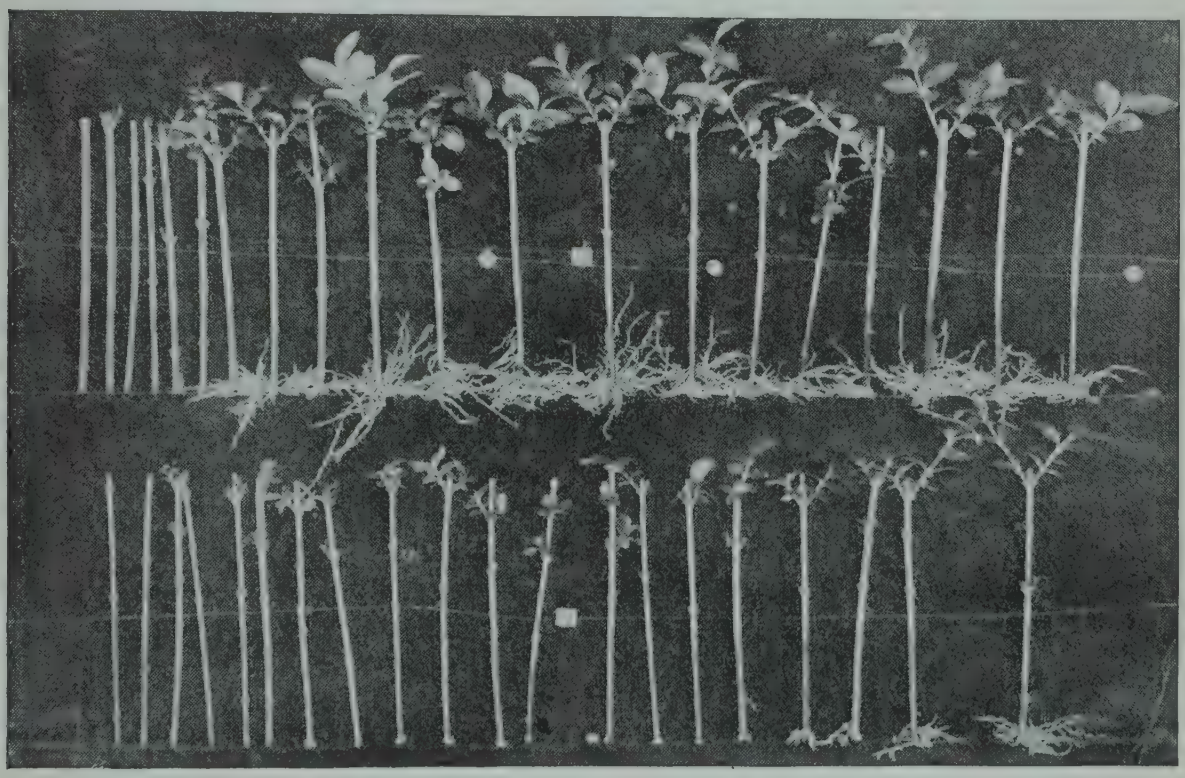

FIG. 4. EFFECT OF TREATMENT OF LIGUSTRUM WITH POTASSIUM PERMANGANATE UNDER RATHER ADVERSE CONDITIONS

Upper row: Cuttings treated for twenty-four hours with 0.1 mol. $KMnO_4$, then placed in sand
Lower row: Check. Cuttings left for twenty-four hours in tap water, then placed in sand

TABLE 4. EFFECT OF TREATMENT OF LIGUSTRUM WITH POTASSIUM PERMANGANATE UNDER RATHER ADVERSE CONDITIONS

(Duration of experiment, March 16 to June 13, 1915. Twenty cuttings in each treatment)

| Treatment | Total dry weight of roots of 20 twigs (grams) | Dry weight of roots relative to check as unity | Total dry weight of tops of 20 twigs (grams) | Dry weight of tops relative to check as unity |
|---|---|---|---|---|
| Check — 24 hours in water, then placed in sand | 0.14 | 1.00 | 1.47 | 1.00 |
| 24 hours in 0.1 mol. $KMnO_4$, then placed in sand | 1.67 | 11.93 | 3.16 | 2.15 |

## REASONS OF STIMULATION

### *Possible effect on food supply*

In seeking the cause of the stimulating effect of potassium permanganate on root growth, it was thought possible that the treatment changed the food stored in the stem of the cutting so as to make it available for immediate use. In order to determine whether this was the case, cuttings were treated as in the preceding experiments for twenty-four hours and then placed in flasks of distilled water. Microchemical tests for sugar and starch were made at intervals of two days at first and of from seven to ten days later. In no case was there any loss of starch or production of sugar to be detected until rapid development of callus and roots started. When the callus was well formed, the starch in the immediate proximity of this tissue was disappearing, but no change was visible in the starch content at a distance of from three to four millimeters from the callus. In spite of the fact that the food remained unchanged until growth started, the treated twigs showed marked stimulation. When the roots were measured, those on the treated twigs averaged 5.32 times those of the checks — an increase of 432 per cent. It should be pointed out that the method of testing is not delicate enough to permit detection of slight changes in sugar or starch content.

It has occurred to the writer that the precipitation of manganese dioxide in the base of the stem may so clog the tissues as to check the loss of organic matter from the cut end. As a result of this check, more food might be available for root formation. This explanation has not been verified experimentally, but it would seem that it is of minor importance.

### *Relation to rest period*

In many cases cuttings were taken in autumn, when they were still in the resting condition. It seemed possible, therefore, that the treatment might have served to bring either the entire twig or its basal part out of the rest period. If such were the case, the increased root growth might be merely due to the fact that the growth had started earlier in these twigs than in the checks, in which case there would be no true root stimulation.

*Effect on rest period of twig as a whole.*— In order to ascertain the effect of potassium permanganate on the rest period of the twig as a whole, Ligustrum cuttings were made on October 15, 1915, and were given continuous treatment as indicated in table 5. As shown by the

TABLE 5. CUTTINGS OF LIGUSTRUM TAKEN EARLY IN THE REST PERIOD, OCTOBER 15, 1915

(Treatment continuous. To cultures marked *F. N. 0.001 per cent*, Knop's full nutrient solution of that concentration was added)

| Solution | November 29 | | December 18 | | | | March 8 | | | | | March 11 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Root length per twig (in millimeters) | | Root length per twig (in millimeters) | | | Number of twigs with buds showing green or with small shoot | Root length per twig (in millimeters) | | | Top length per twig (in millimeters) | | Dry weight of roots per 10 plants (in grains) | | |
| | Cultures 1 and 2 | Average | Cultures 1 and 2 | Average | Relative to check as unity | | Cultures 1 and 2 | Average | Relative to check as unity | Cultures 1 and 2 | Average | Cultures 1 and 2 | Average | Relative to check as unity |
| Distilled water | 0.7<br>0.0* | .... | 40<br>0* | .. | .... | 0 green...<br>1 shoot... | 428<br>272 | ..... | ..... | 16<br>17 | .... | 0.102<br>0.066 | ..... | ..... |
| Distilled water | 0.5<br>0.0 | 0.40 | 31<br>7 | 26 | 1.00 | 1 green...<br>1 shoot... | 371<br>264 | 334 ±29.4 | 1.00 ±0.09 | 12<br>15 | 15.0 | 0.086<br>0.057 | 0.0778 | 1.00 |
| Distilled water and F. N. 0.001 per cent | 0.0<br>0.0 | 0.00 | 0<br>2 | 1 | 0.04 | ..... | .... | ..... | ..... | .. | .... | 0.044<br>0.056 | 0.0500 | 0.64 |
| Tap water | 0.0<br>0.0 | 0.00 | 24<br>20 | 22 | 0.85 | ..... | 468<br>279 | 374 ±26.6 | 1.12 ±0.07 | 16<br>13 | 14.5 | 0.100<br>0.090 | 0.0950 | 1.22 |
| Tap water and F. N. 0.001 per cent | 0.0 | 0.00 | 21 | 21 | 0.81 | ..... | .... | ..... | ..... | .. | .... | 0.118 | 0.1180 | 1.52 |
| $KMnO_4$, 0.01 mol | 118.0<br>60.0 | 89.00 | 287<br>199 | 243 | 9.35 | 0 green...<br>1 shoot... | 977<br>867 | 922 ±33.5 | 2.76 ±0.10 | 12<br>10 | 11.0 | 0.231<br>0.192 | 0.2115 | 2.72 |
| $KMnO_4$, 0.01 mol., and F. N., 0.001 per cent | .... | .... | 281 | 281 | 10.81 | 0 green... | .... | ..... | ..... | .. | .... | 0.213 | 0.213 | 2.74 |
| $KMnO_4$, 0.004 mol | 64.0<br>28.0 | 46.00 | 106<br>188 | 147 | 5.65 | 1 shoot...<br>1 shoot... | .... | ..... | ..... | .. | .... | 0.154<br>0.185 | 0.1695 | 2.18 |
| $KMnO_4$, 0.004 mol., and F. N., 0.001 per cent. | 8.5<br>0.0 | 4.25 | 106<br>34 | 70 | 2.69 | 1 shoot...<br>1 shoot... | .... | ..... | ..... | .. | .... | .... | ..... | ... |
| $KMnO_4$, 0.001 mol | 24.0<br>4.0 | 14.00 | 125<br>41 | 83 | 3.19 | 0 green...<br>1 shoot... | .... | ..... | ..... | .. | .... | 0.121<br>0.115 | 0.1180 | 1.52 |

*Not included in average.

table and by figures 5 and 6, the treatment with potassium permanganate markedly increased root growth but had little or no effect on the tops.

In the cultures with 0.01 and 0.001 molecular potassium permanganate, the roots were visible about ten days earlier than they appeared in the checks. This might seem to have been due to an effect on the rest period. If this were the case, however, the treatment had not affected the whole

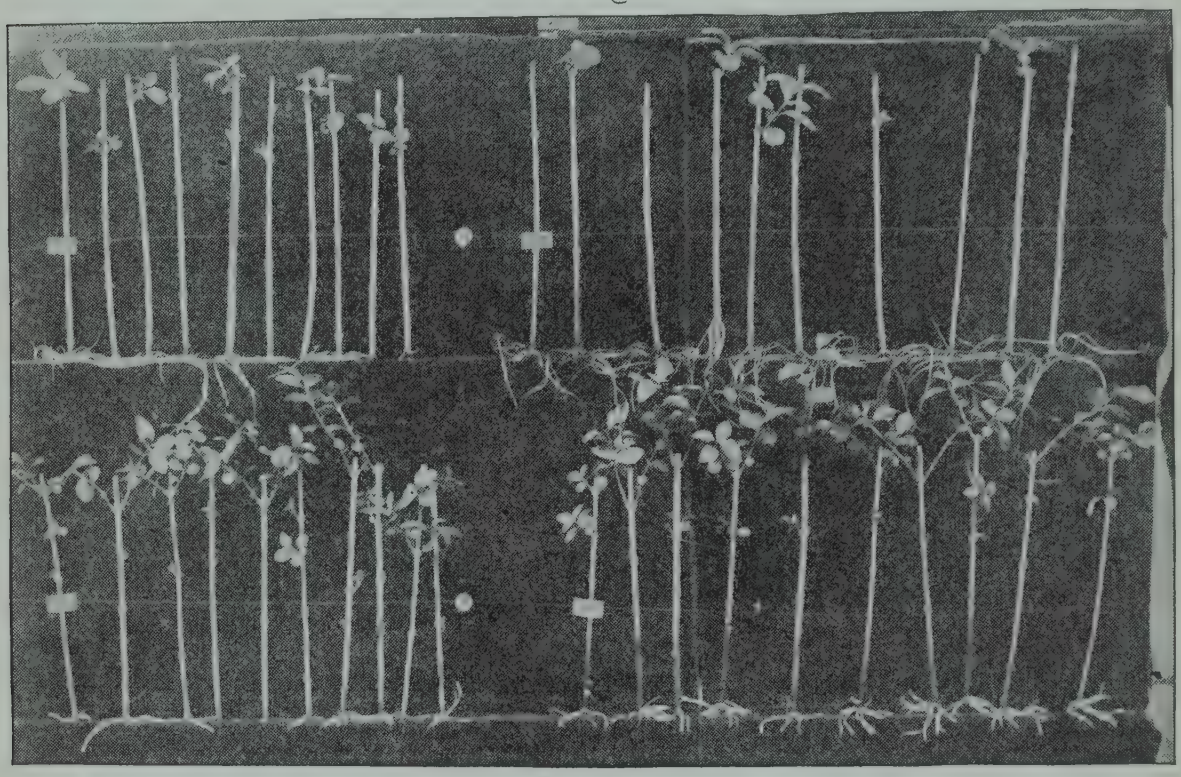

FIG. 5. RELATION OF STIMULATION TO REST PERIOD

Upper row: Cuttings taken early in rest period, October 15, 1915. Twigs at left, check twigs, kept continuously in distilled water until December 27, then placed in tap water. Twigs at right kept in 0.01 mol. $KMnO_4$ until December 27, then placed in tap water. The buds are just starting to grow in both lots, showing approximately equal growth, while the root growth is very much greater in the treated twigs

Lower row: Cuttings taken at end of rest period, on December 8. Twigs at left, check twigs, left for twenty-four hours in distilled water, then transferred to flasks containing distilled water. Twigs at right, treated for twenty-four hours in 0.1 mol. $KMnO_4$, then transferred to flasks containing distilled water. The shoots are well formed in both sets, while the roots have not grown so far as in the twigs shown above. Both roots and tops showed better growth in the treated twigs

twig, for, tho a few buds were started by December 18, these were equally developed on all the twigs whether treated or not. Altho these few buds opened by December 18, most of the buds did not grow until about the first of March. The equal development of the buds indicates that the treatment has no effect on the resting condition of the whole twig.

*Effect on rest period of basal part.*— The only possibility remaining, so far as an effect on the rest period is concerned, is that the treatment

may have started growth in the basal part, leaving the tops dormant, for in some instances the roots of the treated twigs started from three to ten days earlier than those of the checks. This difference in time of starting, however, is insufficient to account for the great difference in growth.

As shown by table 5, the roots of the treated twigs when they had been visible less than two weeks (on November 29) showed growth more than three times that in the checks when the roots of the latter had been visible for at least three weeks (on December 18). Furthermore, as a result of the exposure on November 29, when the cultures were being photographed, the roots in the permanganate cultures were partly broken and dried, so that when measured the second time many of the roots first formed were completely rotted or the ends had died back and new branches were starting. The checks were not injured for no roots had started at that time. In spite of this injury to the treated twigs, the growth was much better in these than in the checks and continued better as long as the cultures were kept. This great difference in root length at the time of the final measurements, which were taken more than twelve weeks after growth had commenced, cannot be explained on the ground that the treated twigs had a start of ten days.

*Stimulation of root growth in twigs that have passed the rest period.*— The following experiments furnish additional proof that the stimulation of root growth by potassium permanganate has nothing to do with the rest period. Cuttings of Ligustrum were taken on December 8, 1915. The bushes from which they were taken had been twice subjected to several days of freezing weather, and, as is brought out later, these twigs had passed out of the resting condition. One hundred and fifty twigs were treated for twenty-four hours in water, and the same number in 0.1 molecular potassium permanganate. After being rinsed, duplicate lots of ten twigs from each treatment were placed in distilled water in a cool room at a temperature of from 5° to 10° C., thirty twigs of each treatment were placed in sand in a somewhat warmer, shaded greenhouse at from 10° to 15° C., and one hundred twigs of each treatment were placed in sand in a still warmer, unshaded greenhouse at from 18° to 22° C.

The buds of the twigs in the warmest house started almost immediately after the cuttings were set out. They were not in the resting condition, and the treated and the untreated twigs started equally; but by the

last of January, when this lot was taken up, the twigs treated with potassium permanganate showed accelerated top growth. No actual measurements were taken of this lot, but the root growth was fully twice that of the checks. The buds of the lot placed in sand in the shaded house opened soon after these. There was no apparent difference in time of starting between the treated and the untreated twigs, but at the end of about ten days those treated with potassium permanganate clearly showed increased top growth. Similar results were obtained with the cuttings placed in water in the cool room.

Results obtained from experiments conducted in the spring of 1917 were very similar to those just described. On cuttings treated either continuously or for a limited time with potassium permanganate, an increased growth of roots ranging from 2.17 to 11.93 times that in the checks was produced. Results following the placing of the cuttings in sand after treatment for twenty-four hours in 0.1 molecular potassium permanganate are shown in figure 4 (page 87).

The buds on all the twigs in these experiments opened very soon after the twigs were set out, and even before the roots started. For this reason the stimulation cannot be explained as due to an effect which may bring the basal part of the twig out of the resting condition and leave the tops dormant. These twigs apparently had completely passed the rest period, and therefore any stimulation obtained cannot have been due to an effect on the rest period. Furthermore, it has been shown by Howard (1915 b), and by other investigators, that, so far as the rest period is concerned, treatments which will exert a stimulating effect if applied during the rest period will have no effect, or may even produce a retarding effect, if applied at or near the end of that period.

*True rest shown only by buds of woody cuttings.*— The effect of stimulation of root growth is evidently independent of the rest period, as already stated. So likewise are callus formation and root development, which proceed in untreated twigs whose buds are dormant. The buds of cuttings taken on October 15 (fig. 5) did not start general growth until about March 1, approximately four months after the cuttings were taken, while the buds of twigs taken on December 8 started almost immediately. Those taken on December 8 were well started by December 22, only two weeks after the cuttings were made and more than two months earlier than those taken on October 15. The roots in the untreated twigs, however,

developed at approximately the same rate whether the twigs were taken before or after the end of the rest period. In both cases the roots were about equally developed forty-five days after the cuttings were made. Very similar results were obtained with cuttings of *Prunus cerasifera*, *Cornus stolonifera* Michx., and *Evonymus europaea*, and with regard to callus formation in *Pyrus malus*.

Cuttings of Evonymus taken in the latter part of September had a strong root system developed by March 1, yet the buds did not break until May 1; while the buds on cuttings taken from the same bush on December 29 started growth within ten days, but as no root system was developed a large number of the twigs withered. Root and callus formation in cuttings, therefore, appear to be independent of the rest period, as stated above. There is a possibility that the wound shock at the cut end brings that part out of the rest period; Howard (1915 b) and other investigators have found that such a stimulus may shorten the rest period. But in some cases the roots develop at some distance from this wounded tissue, and therefore this explanation is insufficient. The cut of course exposes the adjacent tissue to better aeration, resulting in a greater oxygen supply as well as a more rapid loss of carbon dioxide, which might serve to start growth in the dormant cambium. When the twig is immersed in water any inhibiting substances may be washed out of the tissues or the ready access of oxygen may oxidize them. Such an explanation is not entirely satisfactory, however, for if the twig is kept in a moist chamber, not only will both cut ends develop a callus but also cork cells will be formed at the lenticels, indicating cellular activity in regions far from the wounded part; yet in no cases do the buds develop, even when submerged in water or when situated very close to the cut end.

Simon (1906) has shown that root and callus formation proceed when the buds are in a resting state. Howard, in his work on shortening the rest period of cut twigs, makes no mention of any effect on their rooting ability. In a report on experiments with several species of potted woody plants (Howard, 1915 b), he states that treatments which stimulated the tops had no effect on root growth. He does not say, however, how he determined this, and he gives no data.

*Possibility that a treatment affecting the rest period may at the same time affect root growth.*— On the other hand, the fact that the stimulation obtained was independent of an effect on the rest period is no proof

that treatments which would affect the rest period might not also have an effect on root growth. In order to test this point, Ligustrum twigs were taken on November 13 and tied in bundles of twenty twigs each. These bundles were suspended in water for two hours, at the depths and temperatures indicated in table 6, and were then placed in sand in the cutting bench. It is to be noted that at each temperature the top

TABLE 6. EFFECT OF WARM-BATH TREATMENT ON DORMANCY AND ROOT GROWTH

(Treatment lasting two hours; (a), from $2\frac{1}{2}$ to 3 centimeters at base immersed; (c), entire twig immersed. Twenty twigs per culture)

| Treatment | Total root length per twig (millimeters) | Order of greatest root growth | Total top length per twig (millimeters) | Order of greatest top growth |
|---|---|---|---|---|
| 1 (a) Check 20° C | 10± 3.8 | 5 | 6±2.3 | 5 |
| 1 (c) Check 20° C | 6± 3.4 | 6 | 4±1.6 | 6 |
| 2 (a) 35° C | 38± 8.9 | 2 | 23±3.8 | 3 |
| 2 (c) 35° C | 20± 6.1 | 4 | 20±3.4 | 4 |
| 3 (a) 40° C | 55±10.8 | 1 | 29±4.1 | 1 |
| 3 (c) 40° C | 35± 7.6 | 3 | 28±4.6 | 2 |
| 4 (a) 45° C | 2± 0.4 | 7 | 3±1.1 | 7 |
| 4 (c) 45° C | 0 | 8 | 0 | 8 |

growth, as well as the root growth, was better in those twigs of which the bases only were immersed. The order of greatest growth of roots follows almost identically that of the greatest growth of tops. The results indicate that some treatments which start or increase growth in the entire twig may correspondingly increase root growth. It does not seem possible, however, to start growth at the base of the twig by the warm-bath treatment and leave the tops dormant.

Very similar results as to root growth were obtained with twigs taken on September 10 and treated in the same manner. No notes as to the effect on top growth, however, were made at that time.

*Effect of treatment on correlation between tops and roots*

Another possibility that has suggested itself is that the treatment may have brought about a change in correlation between tops and roots, an effect that might be due to a divergence of food movement from tops

to roots. The tables already presented show that this is not the case with the permanganate treatment. In the experiment recorded in table 5 (page 89) there is practically no difference between top growth in the treated twigs and in the checks, and yet there is a very great difference in root development (fig. 5, page 90). The results obtained in the warm-bath treatment (table 6), and in four cases in which the twigs were treated with potassium permanganate after the rest period, showed that both top and root growth were better in the treated twigs than in the checks (fig. 5). This proves clearly that in these cases the roots did not develop at the expense of the tops. It is to be noted here that if the treatment is applied early in the rest period it generally has little or no effect on top growth even for some time after the buds start; while if it is applied after the rest period, tho the buds may start equally the shoots of the treated twigs usually soon surpass those of the checks in development, so that the length and the dry weight of both the tops and the roots exceed those of the checks. With the stronger concentrations, however, a point is apparently reached where there is still stimulation of root growth but at the same time a distinct retardation of top growth. This is well illustrated in table 10 (pages 106–7), which shows that the stronger solutions of both potassium permanganate ($KMnO_4$) and ferric chloride ($FeCl_3$) increased root growth but clearly decreased top growth. Weaker solutions stimulated both tops and roots. Accompanying the increased growth of tops and roots there is at first a lessened dry weight of the stem. After continued growth, however, the stems become heavier, probably due to the increased photosynthetic activity of the larger tops.

On the other hand, Faivre (1871) has shown that in some cases the tops may develop at the expense of the roots. He found that after the buds had formed shoots there was insufficient food left in the stem for root formation. The rooting process seems, as a rule, to be slower than growth of tops, so that if the tops are in a condition to grow they will develop faster than the roots and deplete the food supply, or else, as sufficient water for the increased transpiration is not supplied, the shoots will die, causing the twigs to wither at the same time. As stated earlier, cuttings of various species were taken in late autumn before the end of the rest period and were set out in the greenhouse benches. The tops of most of these remained dormant until March or later, while the roots — or the callus in the case of the twigs of Pyrus — proceeded to develop

vigorously. The buds on the twigs of the same forms taken in January started to grow within two weeks after the cuttings were set out. In the majority of such cases the young shoots, as well as the cutting itself, soon withered and died from lack of water. With Ligustrum, however, root development was so rapid that the majority of the twigs remained alive. Whether this is a matter of food distribution or merely a water relation is not clearly shown by these experiments.

*Effect of treatment on respiratory activity*

The explanations of stimulation of root growth which have thus far been discussed have been shown to be insufficient to fully account for the increased growth resulting when cuttings are treated with potassium permanganate. A more probable explanation appears to be that the manganese increases the rate of respiration in the treated twigs or causes more complete oxidation, thereby preventing the accumulation of inhibiting or toxic products of catabolism.

It has long been recognized that good aeration is essential for root growth either of seedlings or of cuttings, and especially of the latter. De Saussure (1804), early in the nineteenth century, pointed out the fact that oxygen is necessary for root growth of seedlings. He grew chestnut seedlings in flasks containing air, nitrogen, hydrogen, and carbon dioxide, respectively. The carbon dioxide was distinctly injurious to the roots, while the other gases did not allow for growth and the roots soon died. It is commonly understood that one of the chief reasons for the practice of soil drainage is to provide better aeration. Stoklasa and Ernest (1908) have shown that poor aeration of root systems leads to the formation of compounds such as acetic and formic acids within the roots, which may result in their death.

Harris (1914) and a number of other investigators have shown that the growth of roots and the depth to which they penetrate are closely correlated with the water content of the soil and the height of the water table. Harris, as well as several other investigators, states that this is probably due to the fact that a high water content excludes oxygen and the lack of oxygen limits root development.

There is apparently an even greater need for good aeration in soils in which cuttings are placed, than exists for seedlings. This fact has been

recognized for some time. Sorauer (1895) lays strong emphasis on the need of aeration, especially for herbaceous cuttings.

Küster (1903) states that cuttings always callus more readily in a moist atmosphere than in water, tho he considers transpiration, as well as oxygen supply, a determining factor.

Klebs (1903) found that cuttings of *Salix pentandra* develop roots only at the cut end of the twig, not thruout its length as do cuttings of *Salix alba vitellina pendula* (Spath.); however, if the cork layer is removed at a point some distance from the cut end, roots will develop in or near this region. He explains this on the theory that water is the determining factor. He suggests that on removal of the impervious cork layer, water enters the twig, and the roots then develop. He does not realize, apparently, that when the twig is immersed the tissues must be practically saturated — certainly of greater water content than those of the basal end when the cutting is suspended in moist air, yet under the latter condition roots will develop freely. The more probable explanation is that the removal of the cork allows for better aeration, thus increasing the oxygen supply at that point as well as supplying an outlet for the carbon dioxide produced in respiration. The work of Appleman (1916) is suggestive in this connection. He found that tubers of *Solanum tuberosum* were caused to sprout when the skins were removed. The results he explains as due to increased permeability to oxygen.

It is very generally known that when potassium permanganate comes in contact with organic matter, manganese dioxide is precipitated and oxygen is liberated. Some of the most recent work on this line is that of Bunzell and Hasselbring (1917), who found that various organic compounds — glucose, alcohol, and others — will decompose potassium permanganate with the formation of manganese dioxide and in some cases a straw-colored solution containing manganese and giving strong oxidase reactions.

The cuttings treated with potassium permanganate were very much blackened by this precipitate of oxide of manganese, which clings firmly to the surface of the twig. Sections of the twig showed the oxide deposited in the xylem cells for a distance of from one to four millimeters from the cut end. They showed also a slight penetration into the cortex cells thruout the length of the immersed part.

Most manganese compounds are active oxygen carriers or are easily changed to such. This is especially true of potassium permanganate and manganese dioxide. The latter, which is precipitated on and in the twigs as just described, will almost instantly blue guaiacum or redden aloin and decompose hydrogen peroxide. It can therefore act as an oxidase, a peroxidase, or a catalase. Bunzell and Hasselbring (1917), as stated above, have found that various organic compounds — glycerin, tyrosine, peptone, glucose, and others — will decompose potassium permanganate, producing a precipitate of manganese dioxide and also a solution containing some manganese which will give oxidase, peroxidase, and catalase reactions. Whatever stimulation was obtained in these experiments was probably due chiefly to this oxide adhering to the walls or precipitated within the cells. It is probable that it was not due to the permanganate itself, as this seemed very toxic to the roots of seedlings or of herbaceous cuttings. In such cases the roots were formed when the purple color was still present in solution. With the woody cuttings, however, all the purple color had disappeared before the roots started, and the solution contained only the dark brown or black oxides of manganese. In continuous treatments the solution may have contained also some manganese available for oxidizing, as found by Bunzell and Hasselbring. In those cases in which the treatment lasted for only a limited time, the twigs were thoroly rinsed before being placed in the final medium, and therefore no permanganate was carried over.

It has been shown by several investigators that manganese is closely associated with oxidation reactions occurring in plants. Bertrand (1897) found it to be an important constituent of the oxidizing enzyme laccase. When a sample of laccase was not very active, its activity was increased by adding a small quantity of manganese sulfate. Schreiner, Sullivan, and Reid (1910) found that the presence of manganese markedly increased oxidation by soils and by plant roots. This occurs, however, only in neutral or alkaline soils (Skinner and Reid, 1916). McHargue (1914) found manganese to be especially abundant in the seed coats of various seeds next to the cotyledons, and suggested that it played an important rôle in respiratory activities during germination. He found that the oxidase activity of different parts of seeds, tubers, roots, and stems varied directly with the manganese content. Kastle (1910:122–131) cites sev-

eral instances in which investigators have found that manganese is important in the action of a number of oxidases.

It would therefore seem reasonable to explain the marked stimulation obtained with treatment by potassium permanganate as due to the effect of the manganese dioxide, deposited on and in the twig, on the respiratory activity of the cutting, either by directly hastening respiration or by causing more complete oxidation and thereby preventing the accumulation of partially oxidized, toxic, or inhibiting products of catabolism. Such an effect occurring within the tissues would be very similar to that which may occur in the external medium in the presence of microorganisms, as discussed later.

The lack of stimulation with certain forms, notably Salix, may be explained on the theory that the oxygen supply does not become a limiting factor with such forms, and therefore, as the effect of the manganese is merely to increase oxidation, no increased growth is to be expected. The fact that Cannon and Free (1917) found Salix to be peculiar in that its roots were uninjured by lack of oxygen or excess of carbon dioxide, lends weight to this explanation.

*Effect of treatment on growth of microorganisms*

The increased growth of roots when cuttings are treated with potassium permanganate cannot be due to any direct effect in keeping the solution sterile and free from microorganisms, altho in experiments with *Pyrus malus*, *Evonymus europaea*, and *Forsythia* sp., and also in other experiments not here reported, the cuttings treated with permanganate remained alive and vigorous for a much longer period without root formation than did the checks. Pyrus twigs remained in good condition for from six to ten months, while most of the check twigs were rotting after from one to three months. On close examination the treated twigs appeared to be heavily coated with a slimy growth of fungi and bacteria, yet they were alive and healthy. The cultures were certainly not sterile; in fact, in one experiment several of the cultures that showed the greatest root growth apparently had a growth of microorganisms even greater than that in the cultures not treated with permanganate. As shown in table 7, the twigs in the culture with 0.004 molecular cane sugar were slimy to a slight extent on December 18, and those in the culture with 0.004 molecular cane sugar plus 0.004 molecular potassium permanganate were

TABLE 7. EFFECT OF TREATMENT ON CONTAMINATION BY FUNGI AND BACTERIA

(Ligustrum cuttings were taken on October 15, 1915, and were grown in the solutions indicated until December 27, when the twigs were rinsed and placed in tap water)

| Solution | December 18 | | March 8 | | | March 11 | | | Notes showing condition on December 18 |
|---|---|---|---|---|---|---|---|---|---|
| | Root length per twig (in millimeters) | | Root length per twig (in millimeters) | | | Dry weight of roots (in grams) | | | |
| | Cultures 1 and 2 | Average | Cultures 1 and 2 | Average | Relative to check as unity | Cultures 1 and 2 | Average | Relative to check as unity | |
| Check — Distilled water | 40.5<br>0.0 | | 428<br>272 | | | 0.102<br>0.066 | | | No bacterial nor fungous growth evident; not slimy to touch |
| Check — Distilled water | 30.5<br>6.5 | 19.4 | 371<br>264 | 334±29.4 | 1.00±0.09 | 0.086<br>0.057 | 0.0778 | 1.00 | No bacterial nor fungous growth evident; not slimy to touch |
| Cane sugar, 0.004 mol. | 4.0<br>1.0 | 2.5 | 170<br>264 | 217±34.9 | 0.65±0.10 | 0.062<br>0.027 | 0.0445 | 0.57 | Some bacterial and fungous growth evident; slimy to touch |
| Cane sugar, 0.004 mol., and $KMnO_4$, 0.004 mol. | 46.0<br>0.5 | 23.3 | 629<br>308* | 629±93.9 | 1.88±0.28 | 0.151 | 0.1510 | 1.94 | Heavy growth of bacteria and fungi; very slimy to touch |

*This culture had dried out and the roots and shoots were withered; therefore the results were not included in the average nor was the dry weight taken.

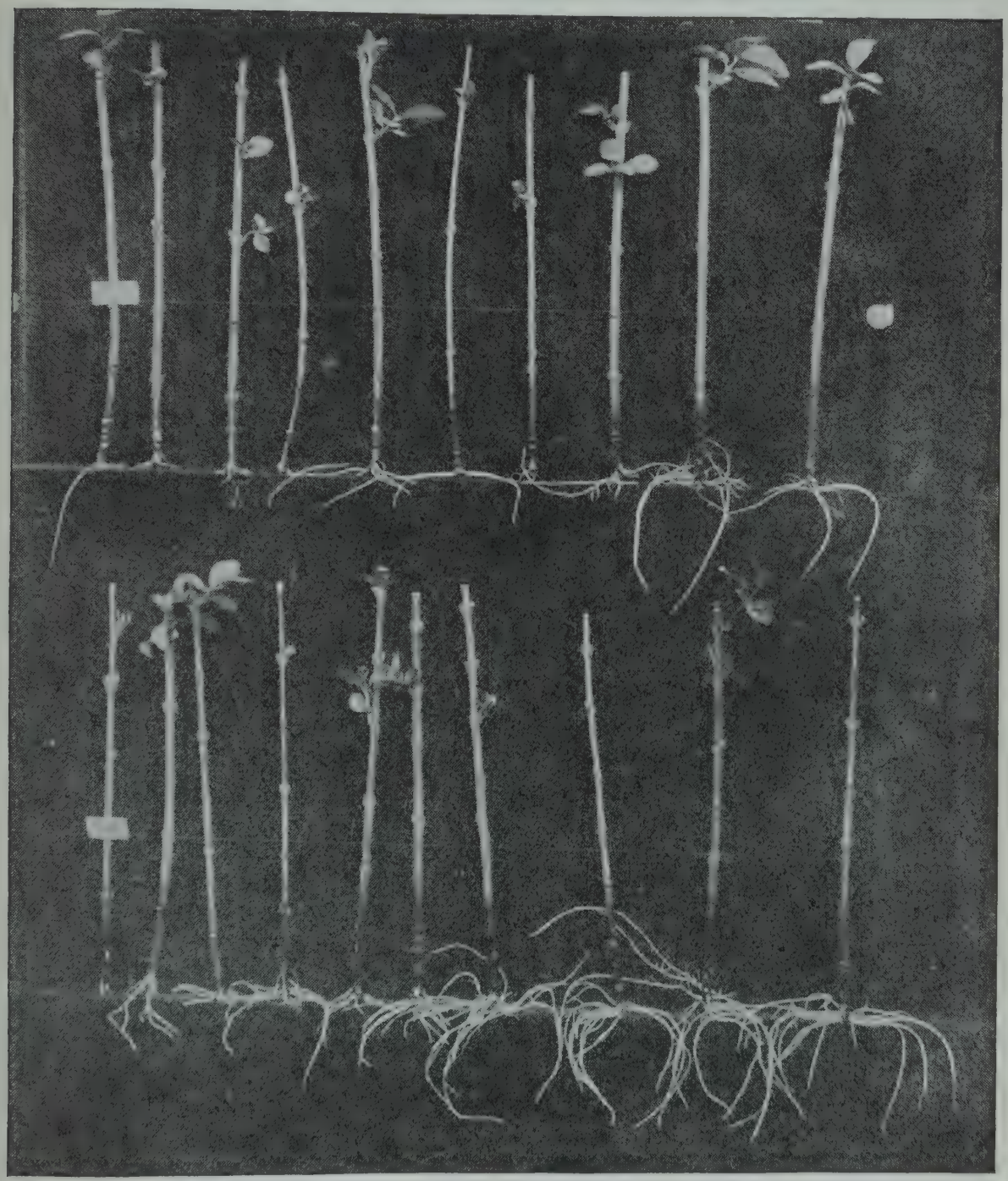

FIG. 6. EFFECT OF TREATMENT WITH POTASSIUM PERMANGANATE ON ROOT GROWTH AS CORRELATED WITH ITS EFFECT ON GROWTH OF MICROORGANISMS

Upper row: Cuttings grown in 0.004 mol. cane sugar
Lower row: Cuttings grown in 0.004 mol. cane sugar with 0.004 mol. $KMnO_4$

much more slimy, with a mat of growth around the stem; yet the roots of the latter were much better developed. When measured later, on March 11, the twigs treated with permanganate and sugar had a root growth 3.39 times that of the twigs treated with sugar alone (fig. 6), which were noticeably less slimy; and the former had a growth 1.94 times that of the plants not supplied with sugar, the stems of which were not slimy to the touch. It would seem, then, that the growth of microorganisms does not of itself injure the cuttings, but that for some reason they become weakened and die, following which fungous growth sets in, attacking the dead twigs.

It is very probable that the presence of soluble organic material allows for a much increased growth of microorganisms, which would result in an increase of carbon dioxide and various toxic compounds and a decrease of oxygen. This increase of carbon dioxide has been found to occur in soils where green crops are plowed under or in ground that has been heavily manured (Boussingault and Lévy, 1852, and Lau, 1906). Kidd (1914) found that the carbon-dioxide content of the soil was very much increased when clipped grass was buried in a pit beneath it; after seven months the soil air of such a pit contained 8 per cent of carbon dioxide. As stated earlier, De Saussure (1804) found that an increased carbon-dioxide content retarded root growth in seedlings. Boehm (1874), Chapin (1902), and Cannon and Free (1917) also have reported retardation of root growth in the presence of carbon dioxide.

It would seem very probable that the increased carbon-dioxide content resulting from the action of microorganisms on the organic material in the medium is injurious to cuttings. Kidd (1914) has shown that carbon dioxide has a retarding effect on respiration, and that this effect is enhanced by a decrease in oxygen content. Microorganisms growing in a medium containing organic matter not only increase the carbon-dioxide content but also decrease the percentage of oxygen. This decreased oxygen supply, coupled with an increased carbon-dioxide content, would tend to retard respiration or to retard the further oxidation of toxic products, thereby causing the death of the twigs, which later might be attacked by saprophytic forms or might be so altered as to be easily attacked by semiparasites.

Furthermore, Chapin (1902) observed that the roots of plants are more resistant to a high carbon-dioxide content than are the tops. This

may partially explain the fact that parts of tops, such as cuttings without roots, are more quickly injured in a soil with a high organic and carbon-dioxide content or a low oxygen content than are rooted cuttings or seedlings. It is certainly true that cuttings are less tolerant of poor aeration. Kidd (1914) found that a rise in temperature lessened the inhibiting effect of carbon dioxide. This might partially explain the beneficial effect of bottom heat, which is discussed later.

In a few preliminary experiments with cuttings inclosed in chambers with increased oxygen content and in chambers with increased carbon-dioxide content, respectively, the cuttings in the increased carbon-dioxide content were distinctly injured, while those in the increased oxygen content remained healthy much longer than did cuttings in normal inclosed air. In none of these preliminary experiments did any of the Ligustrum cuttings remain healthy long enough to form roots. Some very suggestive results, however, were obtained by placing twigs under a suction pump, reducing the pressure by suction, and then replacing the air with carbon dioxide or oxygen. Results from such treatment are illustrated in table 8:

TABLE 8. EFFECT ON ROOT GROWTH WHEN THE GAS IN TWIGS OF LIGUSTRUM IS REPLACED WITH OXYGEN OR CARBON DIOXIDE

(Cuttings taken on March 29, measured on June 2, 1917. Ten twigs to the culture)

| Treatment | Number of cultures used | Roots | | Tops | |
|---|---|---|---|---|---|
| | | Average total length per twig (millimeters) | Relative to check as unity | Average total length per twig (millimeters) | Relative to check as unity |
| Check, untreated..... | 2 | 77.0±18.4 | 1.00±0.24 | 101.6±3.7 | 1.00±0.04 |
| Oxygen..... | 4 | 76.6±15.5 | 0.99±0.20 | 105.6±2.8 | 1.04±0.03 |
| Carbon dioxide*..... | 2 | 1.5± 0.8 | 0.02±0.01 | 76.8±4.7 | 0.75±0.05 |

*Only one twig in each culture was rooted; the others had very weak calluses or none at all.

The twigs were placed under suction for twenty minutes and then allowed to stand in the gas at atmospheric pressure for sixteen hours. They were then removed and placed in flasks of tap water. The single injection of carbon-dioxide gas distinctly retarded both root and top development.

The injurious effects resulting from the presence of organic matter may not be limited to those directly correlated with increased carbon-dioxide or decreased oxygen content. It is very probable that there are certain toxic, partially oxidized substances formed which are directly injurious. In fact, evidences of fermentation and putrefaction were shown by tests for alcohol and by the odor of the solution. Aside from the direct effect of increased carbon-dioxide and decreased oxygen on the respiration of the cuttings, the same condition would tend to increase the production of these partially oxidized toxic substances in the medium. Stimulation by manganese may not be directly due to its effect on respiration of the cutting, as discussed in the preceding pages, but it may be indirectly due to the reduction of toxicity as a result of more complete oxidation carried on either by the cutting or by the microorganisms, or possibly in the solution independent of either. Loew (Loew and Sawa, 1902–03) has suggested a similar rôle for manganese — that it serves to carry on oxidation to completion, thereby preventing the accumulation of toxic, partially oxidized by-products.

## COMPARISON OF THE EFFECT OF POTASSIUM PERMANGANATE WITH THAT OF OTHER MANGANESE COMPOUNDS, AND ALSO WITH THAT OF IRON, OF ALUMINIUM, OF BORON, AND OF PHOSPHORUS

Since manganese dioxide seemed to be one of the active principles in stimulating root growth in the experiments thus far cited, experiments were made to determine whether this compound added directly to the medium would have a similar effect. At the same time other compounds were used which, according to the literature available, had under certain conditions stimulated root growth in seedlings, or which, as in the case of iron, were supposed to have some connection with oxidizing enzymes.

### *Experiments with herbaceous cuttings*

The first experiment was made with tomato cuttings, since these root very quickly and would give an idea as to the approximate concentrations to be used. The stems were not of uniform size but care was taken to distribute them equally. Duplicate cultures of five cuttings each were set up. The roots were measured six days after the cuttings were started, with the results shown in table 9:

TABLE 9. COMPARISON OF THE EFFECT OF VARIOUS STIMULANTS ON THE ROOT GROWTH OF TOMATO CUTTINGS

(Duration of experiment, July 31 to August 6. Five cuttings to the culture)

| | Solution | Total root length per cutting (in millimeters) | | Average | Order of growth |
|---|---|---|---|---|---|
| | | Culture 1 | Culture 2 | | |
| 1 | Check — Distilled water | 49 | 33 | 41± 6.0 | 17 |
| 2 | Check — Tap water | 178 | ..... | 178± 32.9 | 15 |
| 3 | $MnO_2$, 0.1 mol | 822 | 776 | 799±104.4 | 6 |
| 4 | $MnO_2$, 0.01 mol | 969 | 546 | 757± 75.9 | 8 |
| 5 | $KMnO_4$, 0.001 mol.* | 0 | 0 | 0 | |
| 6 | $MnSO_4$, 0.002 mol | 0 | 0 | 0 | A few roots above the solution |
| 7 | $MnSO_4$, 0.0005 mol | 60 | 80 | 70 | 16 (roots mostly above solution, tips brown) |
| 8 | $MnSO_4$, 0.00002 mol | 679 | 715 | 697± 7.8 | 9 |
| 9 | $NaH_2PO_4$, 0.05 mol | 0 | 0 | 0 | Dead |
| 10 | $NaH_2PO_4$, 0.01 mol | 629 | 587 | 608± 67.2 | 13 |
| 11 | $NaH_2PO_4$, 0.002 mol | 589 | 688 | 638± 65.6 | 11 |
| 12 | $H_3BO_3$, 0.001 mol | 922 | 1,034 | 978±145.4 | 3 |
| 13 | $H_3BO_3$, 0.0001 mol | 1,095 | 1,015 | 1,055± 91.3 | 2 |
| 14 | $H_3BO_3$, 0.00001 mol | 1,307 | 1,070 | 1,189± 82.4 | 1 |
| 15 | $FeCl_3$, 0.001 mol.* | 0 | ..... | 0 | |
| 16 | $FeCl_3$, 0.0001 mol. | 917 | ..... | 917±144.2 | 5 |
| 17 | $CaCl_2$, 0.01 mol | 618 | 680 | 649± 60.1 | 10 |
| 18 | $CaCl_2$, 0.005 mol | 664 | 571 | 617± 52.9 | 12 |
| 19 | $CaCl_2$, 0.001 mol | 637 | 354 | 496± 60.3 | 14 |
| 20 | $CaCl_2$, 0.005 mol., and $H_3BO_3$, 0.0005 mol | 925 | ..... | 925±160.4 | 4 |
| 21 | $NaH_2PO_4$, 0.01 mol., and $MnO_2$, 0.01 mol | 461 | 1,071 | 766±305.5 | 7 |
| 22 | $FeCl_3$, 0.001 mol., and $KMnO_4$, 0.001 mol | 0 | 16 | 8± 3.3 | The few roots present were dead |

* All stronger solutions showed no growth.

The results were more consistent than was to have been expected from the small number of stems used and their lack of perfect uniformity. The four treatments showing the best growth all contained boric acid. Ferric chloride stood fifth, while the three containing manganese dioxide stood next in order followed by manganese sulfate in its weakest solution.

TABLE 10. EFFECT ON LIGUSTRUM OF A VARIETY OF COMPOUNDS IN CONTINUOUS TREATMENT

| Period and conditions | Solutions | Root length per twig (in millimeters) | | Top length per twig (in millimeters) | |
|---|---|---|---|---|---|
| | | Average | Relative to check as unity | Average | Relative to check as unity |
| April 7 to June 2, 1917. Ten twigs to the culture, in duplicate | Check — Distilled water | 9.3± 3.0 | 1.00±0.32 | 72.7±3.5 | 1.00±0.05 |
| | $KMnO_4$, 0.01 mol.*.... | 26.3± 5.1 | 2.83±0.55 | 31.7±3.6 | 0.44±0.05 |
| | $KMnO_4$, 0.002 mol.... | 125.5±15.2 | 13.49±1.63 | 83.0±3.3 | 1.14±0.05 |
| | $MnO_2$, 0.01 mol..... | 53.4± 8.5 | 5.74±0.09 | 83.5±2.6 | 1.15±0.04 |
| | $FeCl_3$, 0.0005 mol..... | 114.3±19.4 | 12.29±2.09 | 48.8±2.8 | 0.67±0.04 |
| | $FeCl_3$, 0.0001 mol..... | 59.0±11.8 | 6.34±1.27 | 83.8±3.4 | 1.15±0.05 |
| | $FeCl_3$, 0.00002 mol..... | 32.8± 9.5 | 3.53±1.02 | 69.8±2.1 | 0.96±0.03 |
| | $Fe_2(SO_4)_3$, 0.00005 mol. | 95.3±15.7 | 10.25±1.69 | 77.0±2.9 | 1.06±0.04 |
| September 10 to October 18, 1915. Ten twigs to the culture | Check — Distilled water | 6.5± 3.5 | 1.00±0.54 | ..... | ..... |
| | $H_3PO_4$, 0.01 mol..... | 0 | 0 | ..... | ..... |
| | $H_3PO_4$, 0.001 mol..... | 14.5± 6.4 | 2.23±0.98 | All roots about 1 cm. above base, no callus | |
| | $H_3PO_4$, 0.0001 mol.... | 25.5± 4.8 | 3.92±0.74 | All but a few of the roots about 5 mm. above base, no callus | |
| | $Al_2Cl_6$, 0.001 mol..... | 0 | 0 | 2 cm. at base of all twigs dead | |

| | | | | | |
|---|---|---|---|---|---|
| | $Al_2Cl_6$, 0.0001 mol..... | 65.0±22.0 | 10.00±3.33 | Roots at base of all but one twig | |
| | $Al_2Cl_6$, 0.00001 mol.... | 27.5±10.0 | 4.23±1.54 | ..... | ..... |
| | $NaH_2PO_4$, 0.01 mol.... | 2.0± 1.3 | 0.31±0.20 | Roots about 2 cm. above base | |
| | $NaH_2PO_4$, 0.001 mol... | 1.0± 0.6 | 0.15±0.09 | Roots about 5 mm. above base | |
| | $CaCl_2$, 0.01 mol..... | 5.5± 2.2 | 0.85±0.34 | Similar to check | |
| | $CaCl_2$, 0.001 mol..... | 6.5± 3.5 | 1.00±0.54 | Similar to check | |
| | $CaCl_2$, 0.0001 mol..... | 3.0± 1.1 | 0.46±0.17 | Similar to check | |
| August 28 to October 6, 1915. Ten twigs to the culture | Check — Distilled water | 65±10.3 | 1.00±0.16 | ..... | ..... |
| | $KMnO_4$, 0.002 mol.... | 91± 6.8 | 1.40±0.10 | ..... | ..... |
| | $MnO_2$, 0.05 mol..... | 36± 4.7 | 0.55±0.07 | ..... | ..... |
| | $MnO_2$, 0.01 mol..... | 54± 6.6 | 0.83±0.10 | ..... | ..... |
| | $MnO_2$, 0.001 mol..... | 46± 7.9 | 0.71±0.12 | ..... | ..... |
| | $H_3BO_3$, 0.01 mol..... | 0 | 0 | ..... | ..... |
| | $H_3BO_3$, 0.001 mol..... | 13± 2.4 | 0.20±0.04 | ..... | ..... |
| | $H_3BO_3$, 0.0001 mol.... | 101±11.0 | 1.55±0.17 | ..... | ..... |
| | $H_3BO_3$, 0.00001 mol... | 98±10.0 | 1.51±0.16 | ..... | ..... |
| | $FeCl_3$, 0.0001 mol..... | 76± 8.3 | 1.17±0.13 | ..... | ..... |
| | $FeCl_3$, 0.00001 mol.... | 76± 9.4 | 1.17±0.14 | ..... | ..... |

* As the solution was too strong, no callus was formed at the base and all the roots were formed from 2 to 5 millimeters from the end of the twig. It should be noted also that tho the root growth is greater than in the check, the top growth is much reduced. Weaker solutions stimulated both roots and tops. Comparable results were obtained with strong and weak solutions of $FeCl_3$.

TABLE 11. EFFECT OF TREATMENT OF LIGUSTRUM CUTTINGS FOR TWENTY HOURS WITH VARIOUS STIMULANTS
(Duration of experiment, November 26 to February 9)

| Solution | In distilled water, ten twigs to the culture | | | | | | | | In sand | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Root length per twig (in millimeters) | | | | Top length per twig (in millimeters) | | | | Number of twigs to the culture | Root length per twig (millimeters) | Root length relative to check as unity | Top length per twig (millimeters) | Top length relative to check as unity |
| | Culture 1 | Culture 2 | Average | Relative to check as unity | Culture 1 | Culture 2 | Average | Relative to check as unity | | | | | |
| Check — Distilled water | 53 | 48 | 51 ± 5.8 | 1.00 ± 0.11 | 67 | 69 | 68 ± 1.9 | 1.00 ± 0.03 | 8<br>8 | 56<br>53<br>55 ± 7.6 | 1.00 ± 0.14 | 54<br>55<br>55 ± 3.4 | 1.00 ± 0.06 |
| $KMnO_4$, 0.2 mol. | 181 | 137 | 159 ± 11.7 | 3.12 ± 0.23 | 93 | 95 | 94 ± 2.9 | 1.38 ± 0.04 | 15 | 129 ± 8.9 | 2.35 ± 0.16 | 65 ± 2.4 | 1.18 ± 0.04 |
| 0.1 mol. | 179 | *132 | 156 ± 9.5 | 3.06 ± 0.19 | 87 | 116 | 102 ± 4.5 | 1.50 ± 0.07 | 10 | 135 ± 10.5 | 2.45 ± 0.19 | 63 ± 2.3 | 1.15 ± 0.04 |
| 0.02 mol. | 122 | 94 | 108 ± 10.0 | 2.12 ± 0.20 | 96 | 96 | 96 ± 4.4 | 1.41 ± 0.06 | 10 | 77 ± 10.7 | 1.40 ± 0.19 | 61 ± 4.2 | 1.11 ± 0.08 |
| $MnSO_4$, 0.05 mol. | 66 | 46 | 56 ± 8.8 | 1.10 ± 0.17 | 70 | 63 | 67 ± 2.9 | 0.99 ± 0.04 | 10 | 29 ± 7.7 | 0.53 ± 0.14 | 29 ± 1.9 | 0.53 ± 0.03 |
| 0.01 mol. | 83 | 64 | 73 ± 7.9 | 1.43 ± 0.15 | 90 | 82 | 86 ± 3.6 | 1.26 ± 0.05 | 12 | 39 ± 14.4 | 0.71 ± 0.26 | 51 ± 4.7 | 0.93 ± 0.09 |
| 0.001 mol. | 95 | 72 | 83 ± 8.7 | 1.63 ± 0.17 | 76 | 77 | 77 ± 2.7 | 1.13 ± 0.04 | 10 | 84 ± 12.1 | 1.53 ± 0.22 | 55 ± 2.5 | 1.00 ± 0.05 |
| $H_3BO_3$, 0.01 mol. | 3 | 5 | 4 ± 1.0 | 0.08 ± 0.02 | 68 | 62 | 65 ± 3.1 | 0.96 ± 0.05 | 10 | 0 | 0 | 9 ± 2.5 | 0.16 ± 0.05 |
| 0.001 mol. | 46 | 60 | 53 ± 6.1 | 1.05 ± 0.12 | 71 | 75 | 73 ± 3.1 | 1.07 ± 0.05 | 10 | 30 ± 6.7 | 0.55 ± 0.12 | 32 ± 4.4 | 0.58 ± 0.07 |
| $H_2O_2$, 1.35 per cent. | 4 | 8 | 6 ± 1.5 | 0.12 ± 0.03 | 48 | 50 | 49 ± 1.8 | 0.72 ± 0.03 | 10 | 0 | 0 | 7 ± 1.8 | 0.13 ± 0.03 |
| 0.675 per cent. | 14 | 16 | 15 ± 2.5 | 0.29 ± 0.05 | 54 | 53 | 54 ± 2.2 | 0.79 ± 0.03 | 10 | 0 | 0 | 7 ± 2.8 | 0.13 ± 0.05 |
| 0.27 per cent. | 85 | 52 | 68 ± 6.9 | 1.33 ± 0.14 | 73 | 70 | 72 ± 2.8 | 1.06 ± 0.04 | 10 | 17 ± 6.8 | 0.31 ± 0.12 | 13 ± 3.6 | 0.24 ± 0.07 |
| 0.054 per cent. | 30 | 111 | 71 ± 7.5 | 1.39 ± 0.15 | 57 | 75 | 66 ± 3.1 | 0.97 ± 0.05 | 10 | 25 ± 9.8 | 0.45 ± 0.18 | 11 ± 4.4 | 0.20 ± 0.07 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| $Na_2B_4O_7$, 0.01 mol..... | Dead | .... | ..... | ..... | .... | ..... | ..... | |
| 0.001 mol..... | 8 | 12 | 10 ± 2.9 | 0.20 ±0.05 | 72 | 49 | 61 ±3.7 | 0.90 ±0.05 |
| 0.0001 mol.... | 46 | 60 | 53 ± 6.9 | 1.04 ±0.14 | 70 | 80 | 75 ±4.1 | 1.10 ±0.06 |
| $H_3PO_4$, 0.01 mol..... | 10 | 22 | 16 ± 2.1 | 0.31 ±0.04 | 51 | 71 | 61 ±2.5 | 0.90 ±0.04 |
| 0.001 mol..... | 60 | 72 | 66 ± 7.3 | 1.29 ±0.14 | 76 | 73 | 75 ±3.5 | 1.10 ±0.05 |
| $Al_2Cl_6$, 0.005 mol..... | 29 | 23 | 26 ± 4.1 | 0.51 ±0.08 | 69 | 68 | 69 ±2.3 | 1.01 ±0.03 |
| 0.001 mol..... | 59 | 37 | 48 ± 6.5 | 0.94 ±0.13 | 80 | 74 | 77 ±2.6 | 1.13 ±0.04 |

*Culture dried out, dying.

Calcium chloride and sodium acid phosphate, the one alternating with the other, followed in order of growth, while the check cultures in tap and distilled water were last, excepting those solutions that were distinctly toxic. Potassium permanganate was strongly toxic at the concentrations used. The weakest solution of ferric chloride alone showed marked stimulation. Apparently distilled water also was toxic, as the roots of the cuttings were stunted and produced short, thick branches. It is interesting to note that a supposedly toxic substance, such as boric acid, so markedly stimulates growth when alone in distilled water, especially when the latter itself is toxic.

In another experiment in which Iresine cuttings were placed in solutions of boric acid and ferric chloride, the latter caused greatly increased root growth while the former showed little or no effect.

*Experiments with woody cuttings*

*Continuous treatment.*— Cuttings of Ligustrum were placed at different times in various concentrations of the following compounds: $FeCl_3$, $Fe_2(SO_4)_3$, $MnSO_4$, $MnO_2$, $H_3BO_3$, $H_3PO_4$, $NaH_2PO_4$, $CaCl_2$, $Al_2Cl_6$. The results in some cases were rather irregular. Manganese sulfate was usually toxic in these continuous treatments, but only a few concentrations were tried. Manganese dioxide showed stimulation in three experiments, had little effect in two, while in a sixth retardation was evident. Iron, either as $FeCl_3$ or $Fe_2(SO_4)_3$, clearly showed stimulation in each of the three experiments in which it was used. Boric acid ($H_3BO_3$) indicated stimulation in two experiments, but in a third showed slight retardation. Phosphoric acid ($H_3PO_4$) caused stimulation in one experiment and injury in another. Aluminium chloride ($Al_2Cl_6$) showed stimulation in the two experiments in which it was used. Some of the results obtained are recorded in table 10 (pages 106–7).

*Limited treatment.*— Cuttings were treated for twenty hours as indicated in table 11. One lot was then placed in sand and another in distilled water. The cuttings in distilled water were kept at a temperature about six degrees (centigrade) lower than the others, which accounts for their slower growth. The results of the limited treatment show a marked stimulation with permanganate and manganese sulfate, as regards both roots and tops. In the cuttings subsequently placed in sand, the boric-acid and hydrogen-peroxide treatments retarded growth.

As shown also by other experiments, manganese sulfate, as well as potassium permanganate, is more toxic when the twigs are placed in sand than when they are placed in water. This is probably due to the fact that when the twigs are rinsed and placed in water, the water further dilutes the small quantity of salt that may be carried over; while when the twigs are placed in sand, any such salt is not diluted but is perhaps concentrated as a result of slight evaporation from the surface of the stem. Weaker solutions of manganese sulfate, however, caused increased growth in the three experiments in which they were used.

## DISCUSSION OF STIMULATION BY COMPOUNDS OTHER THAN POTASSIUM PERMANGANATE

Tho the results are not conclusive in all cases, there are at least indications of root stimulation in cuttings treated with $MnSO_4$, $MnO_2$, $FeCl_3$, $Fe_2(SO_4)_3$, $Al_2Cl_6$, $H_3PO_4$, and $H_3BO_3$. The writer has found no references in literature concerning the effect of inorganic compounds on the root growth of cuttings. There are reported, however, a number of instances showing that certain of the above-mentioned substances have served to increase root growth in seedlings. A few of these are here considered.

### *Manganese*

Loew (1904–05) reports that marked stimulation of roots of radishes resulted from the addition of manganese sulfate at the rate of 94 grams per square meter of soil. The treatment had no effect on top growth. Loew, as well as some of his Japanese students, reported several experiments indicating stimulation by manganese compounds, but no other mention is made of their effect on root growth. Furthermore, many of the conclusions are not very reliable, as they are based on results obtained with only a few individual plants with no duplication.

Micheels and De Heen (1906) report that colloidal suspensions of manganese have a marked stimulating effect on the roots of germinating wheat. Colloidal tin also has a stimulating effect on the roots of germinating peas, buckwheat, oats, and wheat (Micheels and De Heen, 1905), but the stimulation is less marked than that obtained with manganese (Micheels and De Heen, 1906). The seeds used in these experiments were soaked for about twenty-four hours in the solutions and were

then suspended on a netting at the surface of the liquid. The treatment had no apparent effect on the percentage of germination; neither was stimulation obtained when the seeds were soaked for twenty-four hours and then suspended over distilled water. The authors explain the stimulation as due to an enzymatic effect of the colloidal suspension on the reserve food in the seed. They believe that it is purely a catalytic effect of suspended particles, as the metals were not taken up by the plant and the strength of the suspension was not diminished. They state that the stimulation could not have been due to substances in solution, for if the colloids were precipitated by the addition of an electrolyte the effect was nullified. It seems strange that the authors should explain the stimulation as due to the enzymatic effect of the suspension on the reserve food, when the stimulant was not absorbed by the plant and when no effect was produced if, after soaking, the seeds were suspended over distilled water. They did find a much increased root growth, and it would seem probable that this increased growth, with the resulting use of soluble food materials, might indirectly increase the rate of digestion by removing the products of digestion.

Brenchley (1910) found that root development of barley is stimulated when manganese sulfate is added to the nutrient solution.

In the Hawaii station report for 1910, Wilcox (1911) records results obtained by planting various types of crops on the manganiferous soils. He states that corn, rice, and other cereals, tobacco, cotton, legumes, garden vegetables, and fruit trees, all showed more or less of the characteristic yellowing of the tops, but the root systems were peculiar in that the root length and the fineness of small roots were strikingly greater than is found in root systems in ordinary soils. Wilcox says: "Apparently the extreme fineness of the roots is due to the lack of resistance which they meet in penetrating manganiferous soils."

Bertrand (1911) reports an increase in weight of roots of sugar beets, and also an increase in the percentage of sugar, as resulting from the addition of manganese compounds to the soil. He explains the stimulation as due to the increased oxidase activity with the resulting increase in respiration. In earlier publications (1896 and 1897) he showed that manganese is an active principle in various plant oxidases, especially laccase.

The explanation previously given for the effect of treatments with potassium permanganate could be applied to the results obtained with manganese dioxide. The lack of as marked stimulation by the latter may have been due to the fact that the dioxide was not deposited in close proximity to the living tissues, as it was in the treatments with potassium permanganate. In this case the possible oxidizing compounds other than manganese dioxide, which Bunzell and Hasselbring (1917) found in solution after decomposition of potassium permanganate, would not be present.

Kelley (1912), in his work on the manganiferous soils of Hawaii, found a peculiar effect on the roots of plants growing in these soils. In most cases in which the manganese was not present in highly toxic concentrations, the roots were found to be highly developed, as appears from the following statement (Kelley, 1912:34): "Certain other plants, as for instance barley, wheat, oats, and jack beans were found to develop an unusual number of fine rootlets. In the case of barley this was especially noticeable." As stated earlier in the bulletin cited (page 26 of reference), "the root development [of corn] was found to be more extensive than in the normal soil," tho the top growth was retarded.

Lipman (1913), in determining the effects of salts of copper, zinc, and manganese on the growth of wheat and vetch in soil cultures, found that manganese gave the most marked stimulation, resulting in an increase in dry weight of both tops and roots.

Howard (1915b) found increased callusing of twigs of Fraxinus when these were coated with a paste of manganese dioxide. He explains this, however, as due to a heat effect resulting from the absorption of light. As the stems in the experiments here reported were not exposed to light, no such explanation is possible.

The stimulation by manganese sulfate may have been due to the manganese sulfate as such, or possibly to manganese dioxide deposited on or in the stem as a result of a reaction with the organic matter. The roots of plants grown in a solution containing manganese sulfate showed a browning, apparently due to the precipitation of manganese dioxide. Deatrick, in an investigation at this university, as yet unpublished, also found a brown precipitate of the oxide of manganese on the roots of wheat seedlings grown in a solution containing manganese sulfate. The sulfate ion, as well as the manganese, may have played some rôle in the stimulation by manganese sulfate.

*Iron and aluminium*

Bertrand (1911) has stated that compounds of iron, aluminium, and boron may act in a catalytic manner somewhat similar to that of manganese. Micheels (1905) earlier suggested such a possibility. The first two compounds may serve as oxygen carriers. Kastle (1910) cites a number of instances in which investigators have found iron to be closely associated with oxidation processes.

The iron as used in the present experiments was very evidently in the colloidal hydrated condition. When the solution was first made it was colorless, but within a few minutes the orange-yellow color of the suspended hydrate appeared, which was then easily precipitated by the addition of magnesium sulfate. The solution of 0.0001 molecular strength showed a very marked bluing of guaiacum tincture, as did also that of aluminium chloride of the same strength. The lack of stimulation in the limited treatments may possibly be explained as being due to the fact that no precipitate is formed in close proximity to the living tissues, as is the case in treatment with potassium permanganate, and since the action must be more or less continuous the short treatments are ineffectual. Micheels and De Heen (1905) found similar results with colloidal tin. When the seedlings were entirely removed from the solution no stimulation resulted.

*Sulfur*

The stimulation obtained in the single treatment with ferric sulfate may have been due to the iron, as in the experiment with ferric chloride, or possibly the sulfate ion may have had some influence. It has been reported in several instances that sulfates increase root growth of seedlings, tho no explanation of this has as yet been offered.

Rusche (1912) found that as a rule sulfates are the most efficient salts in stimulating root growth in a number of plants. Chlorides, on the other hand, are the most harmful to root growth, while nitrates also have a retarding effect.

The tables given by Shedd (1914) indicate that the addition of certain sulfates increases root growth to a greater extent than it does top growth.

Hart and Tottingham (1915) found that certain plants, especially rape and red clover, show greatly increased root growth on the addition of sulfates. Calcium sulfate was the most efficient in this respect of those used.

*Boric acid*

A few investigators (Agulhon, 1910, and others) have reported that boric acid stimulates root development in seedlings. Brenchley (1914) found that boric acid has a marked stimulating action on the roots of peas, radishes, wheat, and turnips.

*Phosphates*

It is generally understood in field practice that phosphates have a beneficial effect on root growth. This has been reported on by Lawes (1847), Russell (1912), Ames and Boltz (1915), and others. In some preliminary work with seedlings it has been found that phosphates, and especially sodium phosphate, markedly increase root growth of flax, alfalfa, and Canada field pea.

Phosphates are not generally considered as oxygen carriers. Leonid Iwanoff (1910) has found, however, that phosphates increase respiration of living seeds and of seeds killed by treatment with toluol. This was determined by measuring the rate of carbon dioxide production. Dibasic phosphates were more efficient than monobasic. Nicolaus Iwanoff (1911) found that phosphates have no effect on the respiration of living seeds or living stem tips, but that they do increase the carbon dioxide production from tissues that have been killed by freezing or by treatment with toluol. He and others have obtained similar results also with yeast. Dibasic phosphates were very efficient, while monobasic phosphates, on the other hand, retarded carbon dioxide production. Iwanoff has shown that the increase in carbon dioxide production brought about by phosphates is probably due, not to an increase in oxidation. but to an increase in anaerobic splitting.

From experiments with seedlings the writer has found monobasic phosphates to be more efficient than dibasic in stimulating root growth.

Schreiner, Sullivan, and Reid (1910) state that phosphates markedly increase oxidation by roots and soils, but whether the oxidation in this case is a result of increased root activity, or its cause, is not certain. As far as is indicated by the results of the present investigation, phosphates have no marked effect on root growth of woody cuttings. Tho the writer has little proof as to the mechanism or the fundamentals concerned, he is of the opinion that phosphates as contrasted with nitrates may in some way check the continued growth of tops and thus allow for a greater

supply of organic matter to be transported to and used by the roots. The effect on roots, therefore, would be chiefly secondary. This point is being tested experimentally.

## PART II. ORGANIC NUTRITION OF CUTTINGS

### REVIEW OF LITERATURE

Faivre (1871) clearly demonstrated that root formation in woody cuttings is dependent on the food stored in the twig. He found also that this food, as starch, disappears from the cutting when growth starts, apparently being used in callus and root formation, or, if the tops appear first, in their production. He demonstrated that this food passes downward to the roots thru the phloem region. The fact that elaborated food passes downward to the roots thru the phloem tissues was recognized by Knight (1801) early in the nineteenth century. The paper he published at that time states that when a tree is ringed the callus develops only on the upper side of the cut, and that growth of the stem also occurs only above the cut. He explains this on the ground that the food substances used in tissue building come from above. Later (1809) he stated that substances used in forming roots must come down thru the bark region, as roots formed on a ringed twig will develop only above the cut. It was clearly recognized by Sorauer (1895) that the roots of woody cuttings are dependent on a supply of food stored in the twig, and those of herbaceous forms on food supplied by attached leaves. Küster (1903) states that callus formation is dependent on the amount of food available.

Boehm (1883), Meyer (1886), Acton (1890), and others, have shown that severed shoots or leaves, if placed in various sugars and other organic compounds, will absorb some of these and store them as starch in the leaves or the stems. It occurred to the writer, therefore, that possibly immature twigs could thus be caused to take up and store a reserve supply of food. If the food were thus stored, it might be possible to decrease the leaf surface and the light intensity, thus decreasing the attendant labor of regulating humidity and light while retaining the advantages to be gained by using herbaceous or immature twigs. The treatment might also increase the vigor of cuttings that root rather readily, and lengthen the season during which woody cuttings can be taken. It was found that Ligustrum cuttings taken before the middle of October were immature and produced weak plants, while those taken the last of November had passed the rest

period, which resulted in rapid growth of tops when the twigs were placed in the cutting bench. This resulted in no injury to the quick-rooting Ligustrum cuttings, but many slow-rooting forms would fail to root under such conditions. If immature cuttings could be taken early in the autumn and caused to root as well as mature cuttings taken later, they would have a longer time in which to become well rooted before winter and before the end of the rest period.

Figures given by Dachnowski (1914) showing results when tomato cuttings were placed in a large variety of solutions, indicate that the addition of glycocoll markedly increases root growth and that cane sugar has a somewhat similar effect.

Knudson (1916) found that an increase in sugar content of the nutrient solution very markedly increases root growth in various seedlings when grown under sterile conditions. The top growth also is benefited, but the roots respond especially well to an increased supply of carbohydrates.

### EFFECT OF LIMITED TREATMENT WITH SUGAR SOLUTIONS ON IMMATURE TWIGS

#### *Treatment with different concentrations*

On August 30 cuttings were taken from large succulent leaders on Ligustrum bushes. Six leaves were left on each twig, and there were four twigs in a culture. The twigs were placed for three days in the solutions indicated in table 12, after which the leaves were removed and the twigs were rinsed and placed in distilled water.

TABLE 12. EFFECT OF SUGAR SOLUTIONS ON IMMATURE TWIGS

(Duration of experiment, August 30 to October 15, 1915)

| Solution | Average length of roots per twig (in millimeters) | | | |
|---|---|---|---|---|
| | Culture 1 | Culture 2 | Average | Relative to check as unity |
| Check — Distilled water | 4 | 4 | 4± 1.5 | 1.00±0.38 |
| Cane sugar, 1 per cent | 20 | 15 | 17.5± 3.3 | 4.37±0.82 |
| Cane sugar, 5 per cent | 35 | 19 | 27.0± 7.4 | 6.75±1.85 |
| Cane sugar, 10 per cent | 58 | 81 | 69.5±16.3 | 17.37±4.08 |

The table indicates that when unripe succulent twigs are allowed to stand in sugar solutions for a short time, the resulting root growth is markedly increased, the greatest increase in this case being shown by the twigs in the strongest solution.

*Treatment for one day, for two days, and for twelve days*

On the same date as that of the preceding experiment, immature twigs were treated with sugar solutions as indicated in table 13 and were then rinsed and placed in sand in the cutting bench. These twigs were immature terminal parts, less succulent than those used in the preceding experiment. The leaves were removed before the twigs were placed in the solution.

TABLE 13. EFFECT OF DURATION OF TREATMENT WITH SUGAR ON LIGUSTRUM CUTTINGS
(Duration of experiment, August 30 to October 30, 1915)

| Culture | Treatment | Number of twigs used | Number of twigs dead | Average total root length per twig (millimeters) | Average total root length per living twig (millimeters) |
|---|---|---|---|---|---|
| 1 | Distilled water one day | 18 | 9 | 43±11.9 | 86 |
| 2 | Cane sugar, 5 per cent, one day | 19 | 14 | 48±11.5 | 182 |
| 3 | Cane sugar, 5 per cent, two days | 19 | 0 | 183±16.6 | 183 |
| 4 | Distilled water twelve days | 20 | 13 | 6± 2.3 | 17 |
| 5 | Cane sugar, 5 per cent, twelve days | 21 | 0 | 50±11.2 | 50 |

Two twigs of the check and two of those in 5-per-cent cane sugar were sectioned on the fifth day and tested for starch. The checks showed no starch either at the base, at 2 centimeters above the base, or at 15 centimeters above the base, while the twigs from the sugar solution showed starch at all three levels. Sugar must therefore have been absorbed and stored in the twigs as starch. In this lot many of the twigs apparently did not have sufficient food stored to allow for any growth, as ten out of eighteen in the better of the check cultures failed to develop roots. When allowed to stand in a sugar solution for two days or more, sufficient food was stored to allow growth of both roots and tops. The tops were not measured, as the new shoots were very short with but few leaves. The condition of the cuttings at the time when the roots were measured is shown in figure 7.

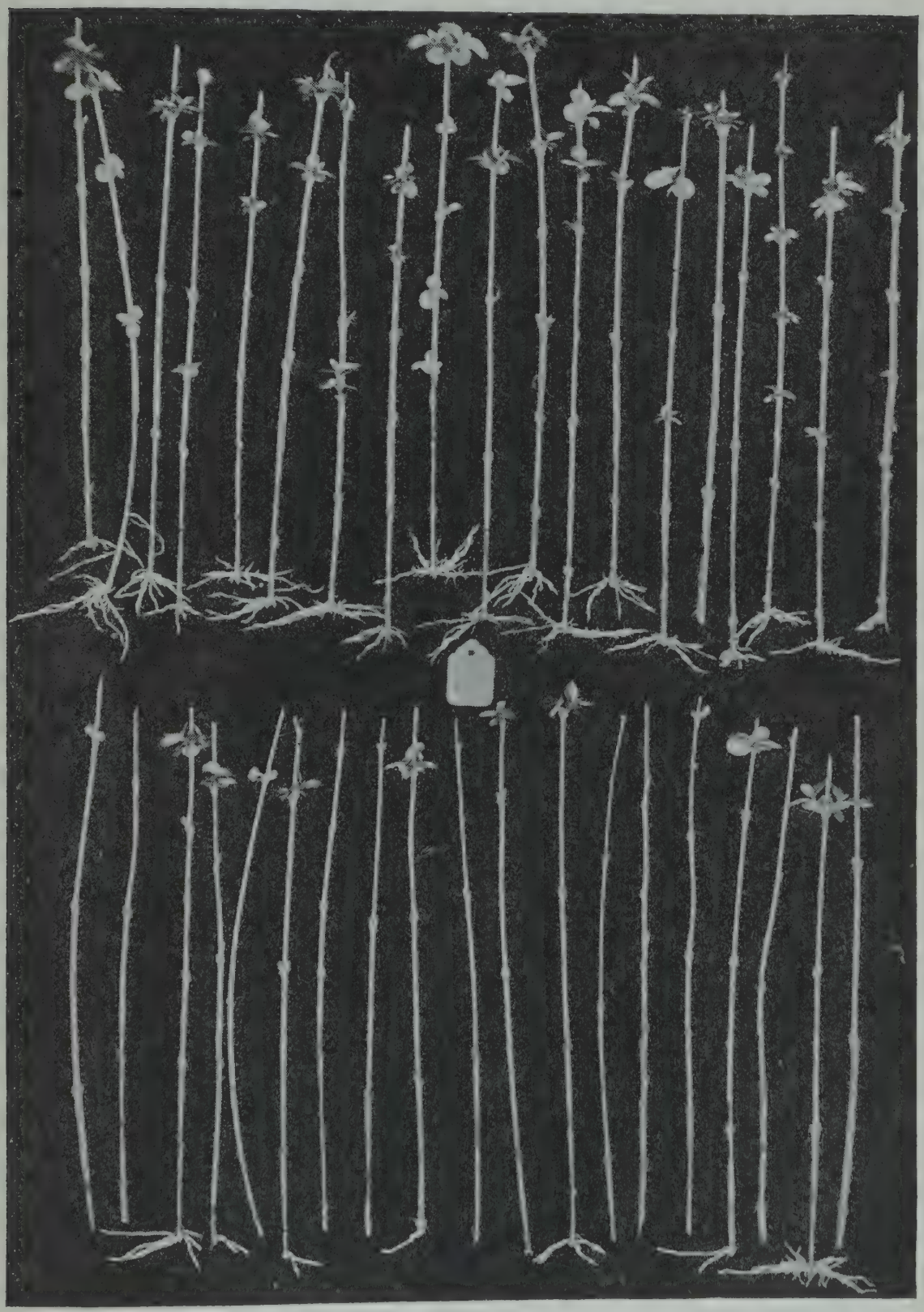

FIG. 7. EFFECT OF SUGAR ON ROOT FORMATION IN IMMATURE TWIGS

Upper row: Cuttings left for two days in 5-per-cent cane sugar, then placed in sand
Lower row: Cuttings left in water for one day, then placed in sand

*Influence of solutions of sugar for one, five, and fourteen days, respectively, in an incubator*

In another experiment more fully ripened cuttings were placed in tumblers containing 100 cubic centimeters of solution, and these were set in incubators at the constant temperatures given in table 14. After the treatment the twigs were rinsed and placed in distilled water.

TABLE 14. INFLUENCE OF SOLUTIONS OF CANE SUGAR AT DIFFERENT TEMPERATURES AND FOR DIFFERENT LENGTHS OF TIME

(Duration of experiment, September 10 to October 30, 1915. Ten cuttings of Ligustrum to the culture)

| Solution | Temperature (centigrade) | Duration of treatment | Root length per twig (millimeters) | Number of twigs rooted | Number of twigs dead |
|---|---|---|---|---|---|
| Distilled water | 30° | 24 hours | 22.0 | 5 | 3 |
| Cane sugar, 5 per cent | 30° | 24 hours | 40.0 | 5 | 2 |
| Distilled water | 35° | 24 hours | 148.0 | 8 | 2 |
| Cane sugar, 5 per cent | 35° | 24 hours | 127.0 | 10 | 0 |
| Distilled water | 30° | 5 days | 165.5 | 8 | 2 |
| Cane sugar, 5 per cent | 30° | 5 days | 268.5 | 10 | 0 |
| Distilled water | 30° | 14 days | 4.5 | 2 | 2 |
| Cane sugar, 5 per cent | 30° | 14 days | 191.0 | 10 | 0 |

In each case at 30° C. the twigs in the sugar solutions showed the greater root development — an increase, as compared to the corresponding check in distilled water, of from 62 to 4144 per cent. At 35°, however, the sugar had a slight retarding effect. In each of the checks from two to three twigs died, while all the treated twigs not only lived but also formed roots, with the exception of two twigs in the 24-hours treatment at 30°. The twigs left in the sugar solution for fourteen days showed a very marked swelling at the base extending from 3 to 4 centimeters above the lower end. This swelling was in the cortex region, which showed also deep longitudinal splits. None of the checks exhibited such swellings. A similar but less pronounced swelling was apparent in most of the twigs used in other experiments when they were left in sugar for several days.

## EFFECT OF CONTINUOUS TREATMENT WITH SUGAR SOLUTIONS

### *Effect of sugar alone on immature twigs*

The experiments just reported indicate that immature twigs left for a short time in sugar solutions will absorb part of the sugar and store it in the stems as starch. The resulting root growth is very much greater than in untreated twigs. The effect of sugar solutions on immature twigs under continuous treatment was studied in the following experiment.

Immature terminal parts of Ligustrum twigs, 20 centimeters long, were taken on September 4, and were treated as indicated in table 15 and then set away in the dark. No roots were developed on the twigs left continuously in 5-per-cent cane sugar. Apparently the growth of microorganisms had produced toxic compounds which inhibited growth. The twigs that were removed from the sugar at the end of eleven days eventually developed roots. All the check twigs died.

TABLE 15. EFFECT OF SUGAR SOLUTIONS ON IMMATURE CUTTINGS OF LIGUSTRUM UNDER CONTINUOUS TREATMENT

(Duration of experiment, September 4 to November 10, 1915)

| Solution | Condition on September 15 | Condition on November 10 | Number of twigs used | Number of twigs dead |
|---|---|---|---|---|
| Distilled water | No starch at base or at 10 cm. above base. Not changed | No roots | 13 | 13 |
| Distilled water | No starch at base or at 10 cm. above base. Changed to fresh distilled water at this time | No roots | 14 | 14 |
| Cane sugar, 5 per cent | Abundant starch at base, less at 10 cm. above base. Not changed | No roots | 14 | 6 |
| Cane sugar, 5 per cent | Abundant starch at base, less at 10 cm. above base. Changed to distilled water at this time | 7 twigs rooted, average length 39 mm. per twig | 14 | 8 |

*Effect of sugar with manganese dioxide, boric acid, or ferric chloride*

Since the cuttings were injured when left continuously in sugar solutions, it was thought possible that the toxicity might be reduced by the addition of some compound which might either retard the growth of bacteria or oxidize toxic compounds produced by them. For that reason the following experiment was undertaken, in which manganese dioxide and boric acid were added to the sugar solutions. On October 6 the twigs in the poorer culture of each pair were rinsed and placed in fresh water. Final notes were taken on December 16, and the results of the experiment appear in table 16.

As shown by table 16, the stronger solutions of sugar retarded or inhibited root growth. The weakest solution, 0.1 per cent, however, caused an increased development. The presence of manganese dioxide resulted injuriously, either when used alone or when combined with sugar. Boric acid, on the other hand, stimulated growth, as has previously been shown. It also partially overcame the inhibiting effect resulting from the presence of sugar.

The retardation of root growth in the presence of sugar is probably due to the formation of some toxic compounds resulting from the action of bacteria and fungi. In several of the cultures alcohol could be detected both by its odor and by iodoform test. Unless the period is too long, the inhibiting effect of sugar continues only as long as the twigs are left in the solution; after being rinsed and placed in fresh water, as indicated by the table, many twigs in which the root growth had formerly been inhibited by the sugar developed normal roots, and judged from their appearance some of these twigs had even greater root development than had the checks.

In another experiment, started on October 15, fully matured cuttings of Ligustrum were allowed to stand continuously in sugar solutions alone, and also in sugar to which was added ferric chloride, boric acid, or manganese dioxide. In every case the presence of sugar varying from 0.04 to 0.0004 molecular strength, retarded root formation. The presence of the inorganic compounds seemed even to increase the retarding effect of the sugar. When potassium permanganate was present with the sugar, however, the retarding effect of the latter was largely overcome.

TABLE 16. INFLUENCE OF SUGAR ALONE, AND TOGETHER WITH $MnO_2$ OR $H_3BO_3$, ON CUTTINGS OF LIGUSTRUM

(Continuous treatment from August 28 to October 6. Ten twigs per culture. On October 6 the poorer culture of each pair was rinsed and placed in fresh water)

| Solution | Root length per twig (in millimeters) October 6 | | | Notes on appearance December 16 | |
|---|---|---|---|---|---|
| | Cultures 1 and 2 | Average | Relative to check as unity | Solution unchanged | Twigs placed in fresh water October 6 |
| Check — Distilled water. | 62<br>67 | 65 ±10.3 | 1.00±0.16 | Fair roots..... | Fair roots |
| Cane sugar, 5 per cent... | 0<br>0 | 0 | 0.00 | Very few roots.. | Large roots |
| 2 per cent... | 6<br>2 | 4 ± 1.4 | 0.06±0.02 | Very few roots.. | Large roots |
| 1 per cent... | 28<br>17 | 23 ± 5.2 | 0.35±0.08 | Very few roots.. | Large roots |
| 0.1 per cent. | 120<br>107 | 114 ± 6.9 | 1.75±0.10 | ..... | ..... |
| $MnO_2$, 0.05 mol..... | 40<br>32 | 36 ± 4.7 | 0.55±0.07 | Fair roots..... | Fair roots |
| 0.01 mol..... | 57<br>50 | 54 ± 6.6 | 0.83±0.10 | ..... | ..... |
| 0.001 mol..... | .....<br>46 | 46 ± 7.9 | 0.71±0.12 | ..... | ..... |
| $MnO_2$, 0.05 mol., and cane sugar, 2 per cent..... | 0<br>0 | 0 | 0.00 | No roots..... | Few roots |
| $MnO_2$, 0.01 mol., and cane sugar, 2 per cent..... | 0.3<br>0.1 | 0.2±0.1 | 0.003±0.002 | Few roots..... | Fair roots |
| $MnO_2$, 0.001 mol., and cane sugar, 2 per cent. | .....<br>0 | 0 | 0.00 | ..... | ..... |
| $H_3BO_3$, 0.001 mol..... | 18<br>8 | 13 ± 2.4 | 0.20±0.04 | Fair roots..... | Fair roots |
| 0.0001 mol..... | 110<br>92 | 101 ±11.0 | 1.55±0.17 | Fair roots..... | Very large roots |
| 0.00001 mol..... | 106<br>90 | 98 ±10.3 | 1.51±0.16 | ..... | ..... |
| $H_3BO_3$, 0.001 mol., and cane sugar, 2 per cent.. | 7<br>3 | 5 ± 1.7 | 0.08±0.03 | Dead..... | Fair roots |
| $H_3BO_3$, 0.0001 mol., and cane sugar, 2 per cent. | 34<br>7 | 21 ± 6.1 | 0.32±0.09 | Few roots..... | Fair roots |

## EFFECT OF LIMITED TREATMENT WITH SUGAR SOLUTIONS ON MATURER CUTTINGS

The experiments thus far reported have shown that beneficial results can be obtained by treating immature cuttings of Ligustrum for from

one to fourteen days with sugar solutions, but that continuous treatment with the same solutions tends to retard root formation in both immature and mature cuttings. The immature cuttings used in the experiments just discussed were found to have little starch stored in the stem. As shown by other experiments, less striking results were obtained when maturer twigs were used. In these experiments, partly matured upper parts of the twigs were used, but these were taken later in the season and had been subjected to several frosts.

Six experiments were set up in which mature Ligustrum cuttings were treated for from two to fifteen days with sugar of from 0.2 to 0.4 molecular concentration. No very marked effects on root growth were obtained at any time when mature cuttings were treated with sugar. Usually the treatment resulted in a somewhat increased top growth, but this was not very striking. There was, on the other hand, a peculiar and marked effect on the nature of the top growth. Normally the buds at the uppermost node of each cutting produce the strongest shoots, while the buds at the other nodes remain dormant or produce only weak shoots. For the twigs treated with sugar, however, there was in each

TABLE 17. EFFECT OF VARIOUS ORGANIC COMPOUNDS ON MATURE CUTTINGS OF LIGUSTRUM

(Twigs cut on December 8, 1915, placed in solution for two days, then rinsed and placed in sand. Buds started on December 27. Measurements taken on March 10, 1916)

| Solution | Number of twigs used | Roots | | Top measurements (in millimeters) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Dry weight per cutting (grams) | Relative to check as unity | Length at first node | Length at other nodes | Total length | Length at each of the first 4 nodes beginning at top | | | |
| | | | | | | | 1st | 2d | 3d | 4th |
| Distilled water | 23 | 0.0440 | 1.00 | 47.0 | 0.4 | 47.4 | 47.0 | 0.4 | 0.0 | 0.0 |
| Glucose, 0.4 mol | 23 | 0.0400 | 0.91 | 26.7 | 21.3 | 48.0 | 26.7 | 20.2 | 1.1 | 0.0 |
| Glucose, 0.2 mol | 24 | 0.0497 | 1.13 | 46.7 | 4.2 | 50.9 | 46.7 | 3.8 | 0.4 | 0.0 |
| Saccharose, 0.4 mol | 24 | 0.0325 | 0.74 | 14.2 | 25.9 | 40.1 | 14.2 | 19.0 | 5.4 | 1.5 |
| Saccharose, 0.2 mol | 25 | 0.0417 | 0.95 | 37.8 | 12.6 | 50.4 | 37.8 | 10.6 | 1.4 | 0.6 |
| Asparagin, 0.25 per cent. | 24 | 0.0361 | 0.82 | 36.3 | 1.3 | 37.6 | 36.3 | 1.3 | 0.0 | 0.0 |
| Peptone, 1 per cent | 26 | 0.0382 | 0.87 | 35.0 | 16.5 | 51.5 | 35.0 | 16.5 | 0.0 | 0.0 |
| Peptone, 0.1 per cent | 26 | 0.0447 | 1.01 | 54.5 | 1.9 | 56.4 | 54.5 | 1.7 | 0.2 | 0.0 |

of the six experiments, especially at the higher concentrations, a partial or total inhibition of shoot formation from the upper nodes, while the second or the third, or even the fourth, node below developed the more vigorous shoots. Similar results after treatment with cane sugar are shown in table 17 and in figure 8. In this case, however, there is no increase in total top growth, as was found in most of the other experiments.

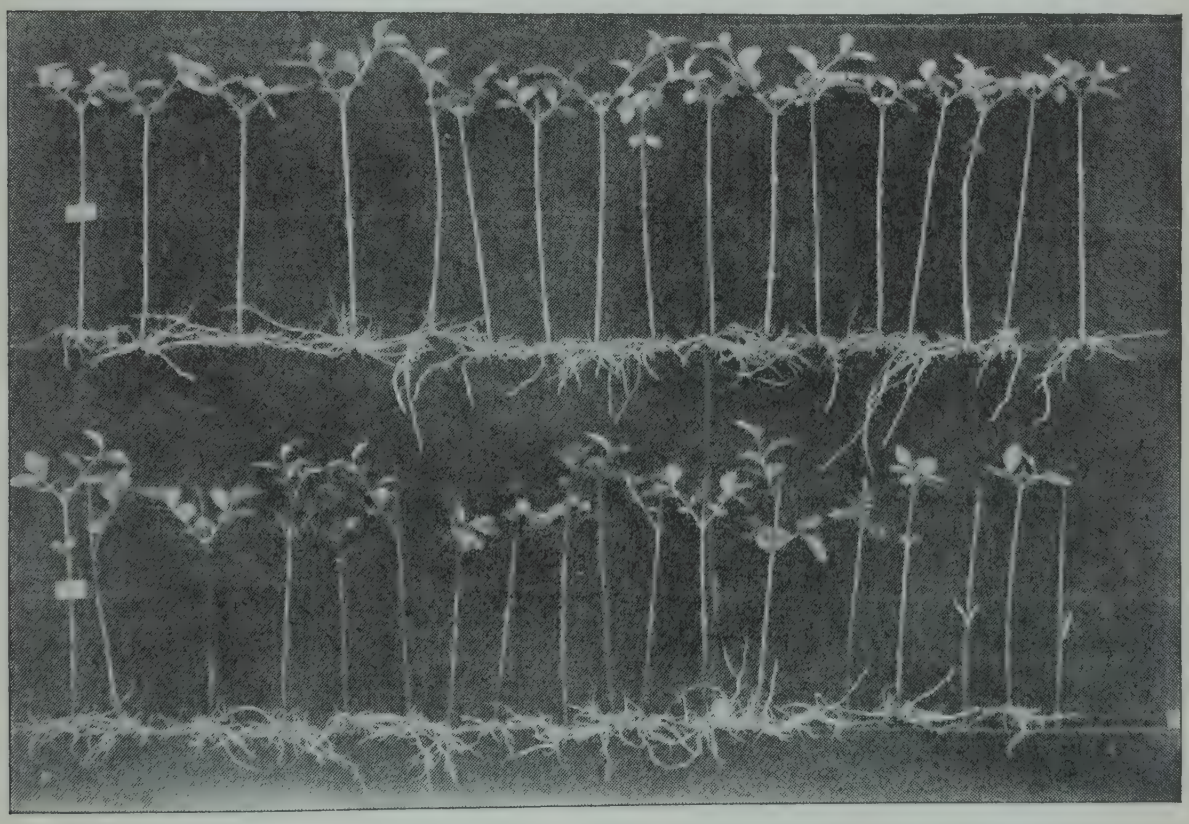

FIG. 8. EFFECT OF SUGAR SOLUTIONS ON MATURE CUTTINGS OF LIGUSTRUM

Upper row: Check twigs left for two days in water, then placed in sand. In nearly every case shoots formed only at the uppermost node

Lower row: Twigs left for two days in 0.4 mol. cane sugar, then placed in sand. In the majority of twigs no shoots were produced at the uppermost node. Root growth was slightly retarded

## FORCIBLE INJECTION OF SUGAR SOLUTIONS

Several preliminary experiments have been carried out in which sugar solutions were forcibly injected into the intercellular spaces of the stems of cuttings. The method is the same as that commonly used to increase penetration of killing fluids. The cuttings were immersed in the solutions, which were contained in heavy glass cylinders, and the pressure was then reduced by means of a suction pump. As a result the gases rapidly

passed out of the stems, and when the pressure was restored the solutions were forced into the air spaces.

Cuttings of tomato and Iresine were found to have absorbed from 5 to 15 per cent of their dry weight of sugar from a 10-per-cent solution, while Ligustrum cuttings took up from 2 to 3 per cent of their dry weight under similar conditions. In one case untreated tomato cuttings contained sugar, measured as hexoses, to the extent of 7 per cent of their dry weight, while the treated cuttings contained sugar, measured as hexoses, to the extent of 17.7 per cent of their dry weight. The treatment, therefore, more than doubled the sugar content. The amount of sugar absorbed was approximately that which would be contained in the volume of solution injected.

As a result of the treatment, cuttings of tomato and Iresine showed an increase in root development over that in the checks. The results obtained with tomato are shown in table 18:

TABLE 18. INFLUENCE OF FORCIBLE INJECTION OF SUGAR SOLUTIONS INTO TOMATO CUTTINGS

| Treatment | Average root length per cutting (millimeters) |
|---|---|
| Water not injected | 166 |
| Water injected | 141 |
| Cane sugar, 0.2 mol., injected | 776 |

In cuttings of Ligustrum taken at the end of the rest period, the forcible injection of sugar caused a distinct retardation in bud development. This retardation was evident in all injected twigs irrespective of the solution used. The twigs treated started bud growth about one month later than twigs not placed under the suction pump, or about forty days after the cuttings were set out; while the buds of the twigs not treated developed in about ten days. Thus the filling of the air spaces with water apparently induces a rest period in twigs that have just passed the normal rest.

## DISCUSSION

The experiments performed with distinctly immature twigs have shown that cane sugar may be taken up by such twigs and stored as starch, and

that these twigs may live and may produce better roots than will untreated twigs. If maturer twigs are used, however, the increase in root growth is not so great and growth may even be retarded, especially if the twigs are placed in water instead of in sand. With these maturer twigs there is usually an increased top growth, and the treatment also determines to a certain extent the node at which the strongest shoot development will occur. Normally the buds at the uppermost nodes develop the strongest shoots, but in twigs treated with sugar the buds lower down are more likely to develop. Even in twigs placed in narrow-necked flasks so that only the uppermost buds were exposed to the light, the lower, darkened buds developed.

Two possible explanations for this unusual development have occurred to the writer. The sugar may increase the concentration within the cells in the lower part of the stem, and this increased concentration and osmotic pressure may reduce the water content of the upper part; in practically all cases the upper part becomes withered and shrunken, but this withering is not evident until some time after the shoots are formed. On the other hand, the presence of sugar near the base may increase the available supply of organic matter for the lower buds, which may therefore grow earlier and more rapidly than the upper buds; this increased growth might result in the loss of both food and water from the upper part.

Howard (1915 b) reports that after the freezing of twigs the basal buds are more likely to develop than are the terminal buds. He found also that mechanical injury near or just below a bud results in the development of that bud. Furthermore, he has shown that mechanical injury increases the sugar content of a twig. In this respect the condition is similar to the sugar treatment here reported. But other conditions do not closely correspond, as the buds of the twigs treated with sugar were not in the resting condition as were those in Howard's experiments. Moreover, the mechanical injury may have increased the permeability, allowing for a loss of carbon dioxide and an increased supply of oxygen. The writer has found that if a twig which has passed the rest period is coated with paraffin, any bud, irrespective of its position, can be induced to develop while all the others remain dormant. This can be done by cutting the paraffin coating in such a way as to allow for aeration. The bud development cannot be explained as resulting from a mechanical weakening of the coat, for the surest way to induce development is to

make an opening thru the paraffin to the leaf scar below a bud. This bud will then develop, breaking thru the unweakened paraffin layer above. This may be one of several factors to be considered in the development of buds at points where the subtending leaf is removed. Loeb (1915) has apparently overlooked this factor of aeration in explaining the development of shoots from buds on the side where a leaf has been removed. He found that even the petiole of a leaf, if left, will inhibit the development of the bud in its axil. It is quite possible that the petiole retards aeration thru the leaf scar.

In twigs left continuously in sugar solutions the rooting ability is usually markedly reduced. This is probably due, primarily, not to the sugar as such, but to the inhibitory by-products resulting from the action of microorganisms on this organic matter. Most of the culture solutions containing sugar for a prolonged period of time became badly contaminated and developed strong odors. In some of them alcohol could easily be detected either by the odor or by the iodoform test. The twigs from such cultures, when thoroly rinsed and placed in fresh water, eventually developed normal roots, and in some cases (tables 15 and 16) these roots were better developed than those of the check cultures. Twigs left in the sugar solutions too long, however, eventually died.

The poor results obtained in common practice when organic matter is present are probably due to the increased production, by organisms, of toxic decomposition compounds and carbon dioxide, and to the lessened supply of oxygen, rather than to the direct effect on the cuttings of the organic matter or of the microorganisms themselves.

Treatment with sugars is apparently of no value when mature twigs are used. Immature twigs, however, may be induced to root much better by such treatment. It would appear from table 12 that solutions stronger than most of those used might be more effective. Meyer (1886) found that leaves of *Beta vulgaris* formed little or no starch when placed in weak sugar solutions of about 1 per cent concentration, while stronger solutions — 10 and 20 per cent — increased starch formation.

When the air spaces of Ligustrum cuttings taken at the end of the normal rest period are filled with water or with sugar or salt solutions, by placing the twigs in the solutions under a suction pump a secondary rest period is apparently induced. It would seem that this excess of water and reduced aeration may favor the production and accumulation

of certain toxic or inhibitory products of catabolism. If this is true it strengthens the belief of the writer that one of perhaps several causes of rest is the accumulation of inhibiting by-products of catabolism, not the accumulation of products of anabolism as suggested by Howard (1915 b). These inhibiting substances may be similar in nature to the "staling" substances produced by fungi as reported by Balls (1908), or to the toxic excreta from roots which have been under investigation by the men of the Bureau of Soils at Washington.

Other experiments on the rest period of plants, on organic nutrition of cuttings, and on this method of injection of organic and other substances, are being conducted, and therefore further data and discussion regarding these topics are reserved until later.

## PART III. GENERAL DISCUSSION WITH REFERENCE TO PRACTICES COMMONLY FOLLOWED BY GREENHOUSE AND NURSERY MEN

In the propagation of plants by cuttings, certain general practices are observed by the majority of workers. The reasons given for such practices may vary widely with the individual growers. Furthermore, many of those most commonly given might be termed popular reasons, and have but very little scientific foundation. In some cases the real significance of the practices is recognized, but in many others the governing principles are apparently very poorly understood. The explanation for some of these practices, in so far as the present investigation has a bearing on them, are here briefly discussed.

It is usually recognized that good aeration is necessary, and for this reason a very porous medium is provided in which to start the cuttings. Sand is perhaps the commonest medium employed. It is generally agreed also that the medium must be well drained. This allows for better aeration, tho many persons think that water as such is directly injurious to the cuttings and may enter into and rot the twigs. Cuttings are sometimes started directly in water, in which case the water is held in shallow pans. These, of course, serve to give better aeration than deeper dishes would afford. In the case of cuttings that have been started in unglazed earthenware pots it has often been noted that those placed near the edge of the pot root better than those near the center. Bailey (1913:50) offers the explanation that the temperature is higher in that region. As an actual fact, however, the temperature near the edge of

the pot is usually lower, due to the cooling effect of evaporation. Bailey suggests further that the deflection of nutrients ("plant food") to that region, due to evaporation, may increase growth. The experiments reported here, however, would contradict this. The more probable explanation, which Bailey also suggests, is that the soil is better aerated in that region. This may explain also the matting of roots next to the walls of the pot in the case of potted plants.

A practice commonly followed in the propagation of dormant cuttings from woody varieties is that of burying the cuttings for a time with the basal ends upward. Various reasons for this practice have been offered. It has been said that sap naturally flows upward, and therefore, if the cuttings are buried with the basal end up, the sap will flow into that part and form roots. Other reasons assigned are that the tops are thus kept dormant, or that the bottoms are thus directly heated (Bailey, 1913:57). It is questionable whether, at the time of year when the cuttings are thus buried, the temperature near the surface of the soil would be higher than that a few inches below. It is conceivable, however, that during the warm days in spring the temperature at the surface may exceed that below. It would seem that a very possible explanation might lie in the fact that twigs so treated would have much better aeration at the basal ends than if buried in an upright position.

Bottom heat is as a rule beneficial to root formation and is very necessary in the propagation of some varieties. This increased temperature, of course, tends to increase respiratory activity in those tissues that produce roots. The upper part of the stem, on the other hand, is left cool and remains in a comparatively quiescent state. When the temperature is approximately equal thruout the length of the stem, the tops of many varieties will develop and root formation is then inhibited. The higher temperature may serve also to decrease the retarding effect of any carbon dioxide that may be present. Such an effect on the germination of seedlings has been shown by the work of Kidd (1914).

It has been shown that the stimulation resulting from treatment with potassium permanganate is largely independent of any effect on the rest period of the twig. Nevertheless it is fairly clear that better results will be obtained with most woody cuttings if these are taken before the rest is over. As a general rule, woody cuttings are taken in the autumn before heavy frosts or freezes set in (Bailey, 1913, and Sim, 1904). One of the

reasons put forward to explain this practice is that at that time of the year the sap is flowing downward and would therefore more readily form roots. The commonest reason given is that the cuttings will root better if a callus is allowed to form during the late autumn or early winter, while if no callus is formed the cutting will not root, or at least will not root so readily.

It would seem, from the results obtained in the present investigation, that this difference in rooting ability between twigs taken in the fall and in the spring is dependent on factors affecting the rest period of the buds, and therefore, indirectly, the food and water supply. Faivre (1871) has pointed out the fact that if woody cuttings are taken in autumn the tops will remain dormant, allowing the roots to form, while if the cuttings are taken in spring the tops will start and use up the stored food which would otherwise be available for root formation. This seems to be the most probable explanation, for, as stated earlier, as a rule the rooting process is slower than the growth of shoots, when the buds are not in the resting condition; the latter therefore develop more rapidly than do the roots, and, as sufficient water for the increased transpiration is not supplied, the shoots wither, causing the whole twig to wither at the same time. The increased top growth also reduces the amount of food available for root formation, as stated above.

Evidently it is not necessary to callus the cuttings before setting them out if they are taken before they have passed the resting stage. Some workers, however, say that the woody forms, which will not be winter-killed, will strike root just as well if left on the parent plant until spring. On the other hand, as the root development and the callus formation are apparently independent of the rest period, the taking of cuttings when the buds are dormant would allow for a longer period for the comparatively slow-growing roots and callus to start development, and thus insure a better root growth. If cuttings are taken in the fall and stored at low temperatures, they may have no apparent root development when set out in the spring and yet it is probable that incipient growth has begun.

Tho stimulation by potassium permanganate has been shown to be independent of an effect on the balance between root and top formation, such a balance can be partially controlled by selecting the right season for taking cuttings, as has just been discussed, or by regulating the tem-

perature. As has already been stated, this balance can be controlled by the application of heat to the basal part of the cutting while the growth of the tops is retarded by continued low temperature.

As stated earlier, it has been recognized that in order to form roots a cutting must have available a sufficient amount of elaborated food. In the case of dormant woody cuttings, this food is stored in the twig, while herbaceous cuttings are dependent on such organic matter as is elaborated by the attached leaves. The practice of ringing the twigs some time before making the cuttings, or ringing or notching before layering, serves merely to increase the supply of this food by checking its removal thru the phloem to other parts of the plant.

The explanation more commonly given for ringing, is that since this practice tends to increase callus formation it correspondingly increases root formation, because a callus must be formed before the roots will develop. As Corbett (1897) has stated, however, and as the writer has observed, callus formation does not necessarily precede or even accompany root formation. Conditions favoring callus development in cuttings favor root formation also, and conditions that hinder or inhibit the former process will usually check the latter. It is true further that if there is insufficient food for vigorous callus production there is a corresponding deficiency for root formation. Vigorous callus development, therefore, is merely an indication that the cutting is in good condition and is well supplied with food, and that the external conditions are favorable for root formation.

In the course of the present investigation it has been shown that immature cuttings of Ligustrum and herbaceous cuttings of tomato, if placed in sugar solutions for a limited time, will absorb sugar from such solutions in sufficient quantities to increase root growth. It has been shown also that if such cuttings are left continuously in the sugar solutions, the root formation is largely suppressed. This inhibition is explained as being due, not to the sugar directly, but to the toxic substances formed as a result of bacterial or fungous action, or to a lessening of the oxygen content coupled with an increase in carbon-dioxide content. As a general rule, propagators are careful to exclude all easily decomposed organic matter from the medium in which the cuttings are to be grown. The explanation usually given for this practice (Bailey, 1913:54) is that the presence of such organic matter supplies a medium in which fungi can grow, and therefore the plants are more liable to damping-off. From the

results found in the present work, it would seem more probable that the organic matter is acted upon by microorganisms, which results in a decrease in the oxygen supply, an increase in carbon dioxide, and the production of toxic or inhibiting by-products. Each factor enhances the inhibiting effect of the others, and the cuttings are thereby killed or weakened and are then attacked by the fungi.

It has been shown further that the presence of nutrients has a detrimental effect on woody cuttings, and that an increase in concentration of a nutrient solution distinctly reduces growth. This offers another suggestion as to the value of sand as a medium for starting cuttings. Such a medium has, as a rule, less soluble nutrients, is better aerated, and is less likely to contain easily decomposed organic matter, than ordinary soil.

## SUMMARY

1. The experiments conducted during the course of the present investigation show that treatments with potassium permanganate may result in a very marked increase in root growth of various woody cuttings. Five possible explanations for this stimulation have suggested themselves to the author. These are: (1) that the treatment causes a change in the nature of the food supply of the twig; (2) that it affects the rest period of the cuttings, serving to start growth earlier and thereby causing an apparent stimulation of root growth; (3) that it upsets the balance of food supply between the tops and the roots in favor of the latter; (4) that it retards or inhibits growth of microorganisms; (5) that it increases respiratory activity by catalytically hastening oxidation. The results obtained show that the last of these is the most probable explanation. The others may in some cases be of importance in explaining the rooting of cuttings, but the stimulation by potassium permanganate cannot be fully explained in such ways.

2. Root growth is largely independent of the rest period, for it appears that only the buds, not the whole stem, assume the resting condition.

3. Manganese dioxide, manganese sulfate, aluminium chloride, ferric chloride, ferric sulfate, boric acid, and possibly phosphoric acid, may at times show a slight stimulating effect on the rooting of cuttings.

4. Nutrient solutions are, as a rule, injurious to root growth in cuttings.

5. Immature twigs can be caused to absorb cane sugar and store it in such form as to be available as a food supply for increased root development.

6. Mature twigs are but slightly benefited, or may even be somewhat injured, by treatment with cane sugar.

7. As a result of placing the base of a cutting in a sugar solution for a short time, the terminal bud of the twig fails to develop in a normal manner and the lower buds form shoots instead.

8. Any injury accompanying treatment with sugar is due, not directly to the sugar, but to the resulting products formed by bacterial or fungous action.

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NOVEMBER, 1918

MEMOIR 15

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# INSECTS INJURIOUS TO THE HOP IN NEW YORK

## WITH SPECIAL REFERENCE TO THE HOP GRUB AND THE HOP REDBUG

I. M. HAWLEY

ITHACA, NEW YORK

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# INSECTS INJURIOUS TO THE HOP IN NEW YORK

## WITH SPECIAL REFERENCE TO THE HOP GRUB AND THE HOP REDBUG

# INSECTS INJURIOUS TO THE HOP IN NEW YORK[1]

## WITH SPECIAL REFERENCE TO THE HOP GRUB AND THE HOP REDBUG

I. M. Hawley

The investigations herein recorded were begun in the spring of 1913 and continued in 1914 and 1915. The greater part of the time was spent in investigating the hop-vine borer (*Gortyna immanis* Guenée) and methods for controlling it. Two new pests, the hop redbug (*Paracalocoris hawleyi* Knight) and the filamented looper (*Nematocampa limbata* Haworth), were also studied, as well as an old but little-known pest, the hop snout-moth (*Hypena humuli* Harris). Some control experiments against the hop aphis (*Phorodon humuli* Schrank) under New York conditions were conducted, and notes were made on a few pests of lesser importance.

### NATURE OF THE HOP PLANT

In order that the relation of these pests to their host plant may be clearly understood, a word should be said regarding the growth and characteristics of the hop.

The growing of hops in the eastern United States is restricted to small sections of New York State, and for this reason the plant is little known. The hop is a perennial plant, the roots living over from year to year and sending up each spring a fresh supply of rapidly growing vines. There are several roots in each hop hill. The hills are from seven to eight feet apart and there are from seven to eight hundred in an acre. The vines must be twined around some sort of support, the commonest form being either poles alone or a series of poles and strings. In some cases two poles and no strings are used, but the commoner method is to have one pole to a hill, with strings running from the middle of each pole to the tops of the ones adjacent to it.

In July and August the main vines send out arms, and on these the hops are borne. The flowers, or burs, are produced the latter part of

[1] Also presented to the Faculty of the Graduate School of Cornell University, June, 1916, as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy. The work was done under the direction of Professor Glenn W. Herrick. The drawings were made by Miss Anna C. Stryke.

July, and the full-grown hops (fig. 9) may be picked from August 20 to the middle of September, depending on variety, weather conditions, and insect and fungous pests. After the hops are picked they are dried and baled, and are then ready for market.

Fig. 9. hops at picking time

Most hops are used in filling the demands of the breweries. Small oval bodies, known as lupulin granules, are formed at the base of each bract, and these contain resins which give the characteristic taste to the beverages for which hops are used.

## THE HOP-VINE BORER, OR HOP GRUB
## (*Gortyna immanis* Guenée)

### GENERIC HISTORY

1852 — Guenée, A., Histoire naturelle des insectes 5:128 ..... Hydroecia
1874 — Grote, A. R., Buffalo Soc. Nat. Sci., Bul. 2:18 ..... Gortyna
1883 — Comstock, J. H., Amer. agr. 42:275 ..... Apamea
1884 — Smith, J. B., U. S. Div. Ent., Bul. 4, o. s.:34 ..... Hydroecia
1885 — Lintner, J. A., New York State Ent., Rept. 2:41 ..... Gortyna
1893 — Smith, J. B., U. S. Nat. Mus., Bul. 44:175 ..... Hydroecia
1897 — Howard, L. O., U. S. Div. Ent., Bul. 7:40 ..... Hydroecia
1902 — Dyar, H. G., List N. A. Lep., p. 175 ..... Gortyna
1909 — Howard, L. O., The hop, p. 128 ..... Gortyna
1910 — Hampson, G. F., Cat. Lep. Phal. 9:41 ..... Hydroecia
1917 — Barnes, W., and McDunnough, J., List Lep. Boreal Amer., p. 69 ..... Gortyna

As may be seen from the preceding list, the generic name of *Gortyna immanis* has been changed many times by systematic workers on this group of noctuids. The reason for the changes has been the question of the type of the genus.

### COMMON NAMES

The common names applied to *Gortyna immanis* are all based on the work of the larva. Dodge (1882) [2] gave the insect its first common name, the hop-vine borer; Comstock (1883) retained this name and added that of hop grub; Fletcher (1893 a) applied a third name, the collar-worm of the hop; and a fourth name, the hop-plant borer, was given by Howard (1897). Among hop growers the larvae are known as hop grubs, or more commonly as grubs.

### DISTRIBUTION

*Gortyna immanis* is a native North American insect and has been widely collected in the northern United States and in Canada (Howard, 1897). Smith (1884) gives for its distribution the northern United States from the Atlantic to the Pacific. The insect is especially abundant in the Eastern States and in Canada where hops are grown. In addition captured moths are reported from the States of Illinois, Colorado, and Washington (Howard, 1897).

In spite of the fact that moths have been taken in the State of Washington, no injury to the hop crop of the Pacific coast is reported in entomological literature. One popular article by Daniel Flint (1882) has been quoted as describing injury by the larva of this insect, but the writer of the present paper believes the work described is that of a boring beetle. The "worm" that did the damage does not conform to the characteristics of a lepidopterous larva.

### HOSTS

So far as known, *Gortyna immanis* is able to reach maturity only on the hop. Evidence exists, however, supporting the possibility of other hosts. In the spring of 1914 a farmer near Waterville, New York, reported that he had occasionally found the young larvae at work in his corn. This report the writer was unable to verify at that time. Larvae placed on young corn plants in the spring of 1915 flourished until the

[2] Dates in parenthesis refer to *Bibliography*, page 219, or to *Literature cited*, page 223.

plants were killed. The work was similar to that on the hop during the early stages, when the larva bores inside the stem.

In the spring of 1915 the young larvae were found very commonly breeding in grass in and around hopyards. Their work on grass is very much like the early work on the hop, and is discussed at some length later (page 156). Cages were placed over five of these grass plants on June 7. On August 17 these cages were examined, and no live larvae, pupae, or adults were to be found. It is assumed, therefore, that the larva cannot mature on grass.

### FINANCIAL LOSS CAUSED

The loss due to the work of the larva of *Gortyna immanis* varies greatly in different years, and in different yards in any one year. In years when the insects are numerous there may result nearly a total loss to some growers. A hop grower in Bristol, New York, informed the writer that he had seen the damage so great that the hops were not picked. Dodge (1882) estimated the loss due to the insect in New York State in 1879 at $600,000.

The writer worked in one yard where there were ninety dead vines in one hundred hills, or a computable loss of twenty per cent from the work of the insect. To this must be added the damage in weakened vines. Judging from the hills inspected, this field had not more than twenty-five hills in an acre in which the grubs had not worked. It is probable that a total loss of forty per cent would be a conservative estimate for this yard.

### NATURE OF THE INJURY

The injury of *Gortyna immanis* to the hop plant may be classed under four phases, depending on the part of the plant attacked: (1) the work in the head of the hop; (2) the early (inside) work in the vines; (3) the late (outside) work on the vines; (4) the work in the roots.

#### *The work in the head of the hop*

Dodge (1882) and later writers on hop insects supposed that the egg of *G. immanis* was laid on the tip of the hop vine early in the spring. It was reported that when the egg hatched, the young larva bored at once into the head, producing a blunted condition known as a muffle

head. As is explained later, this theory of egg laying is incorrect, but it is true that some of the young larvae do find their way into the head of the hop.

Newly hatched larvae of *G. immanis* may crawl long distances and enter any part of the hop plant that is tender enough for their small mandibles, or jaws, to break open. Some of them in their journey reach the head

FIG. 10. HEALTHY AND MUFFLE-HEADED HOP VINES. NATURAL SIZE
The blunted condition of the injured heads on the right should be noted
(Photograph by G. W. Herrick)

of the hop and find a place for easy entrance in the budlike tip. There is no definite place or manner of entrance. Some larvae bore their way into the side of the head, leaving an easily recognizable hole; others enter the tip itself and make their way between the developing leaves; while a few enter the base of the head, or the vine just below the head, causing it to bend to one side. The vines attacked become stockier, and as the

larva feeds on the tender interior tissues, killing the growing point, the head usually takes on a short, thick shape with scraggly leaves, in contrast to the pointed tip with closely folded leaves of a healthy head (fig. 10).

The root of a hop plant sends up fresh vines for a period of several weeks. The writer has noted cases in which, due to late hatching of the

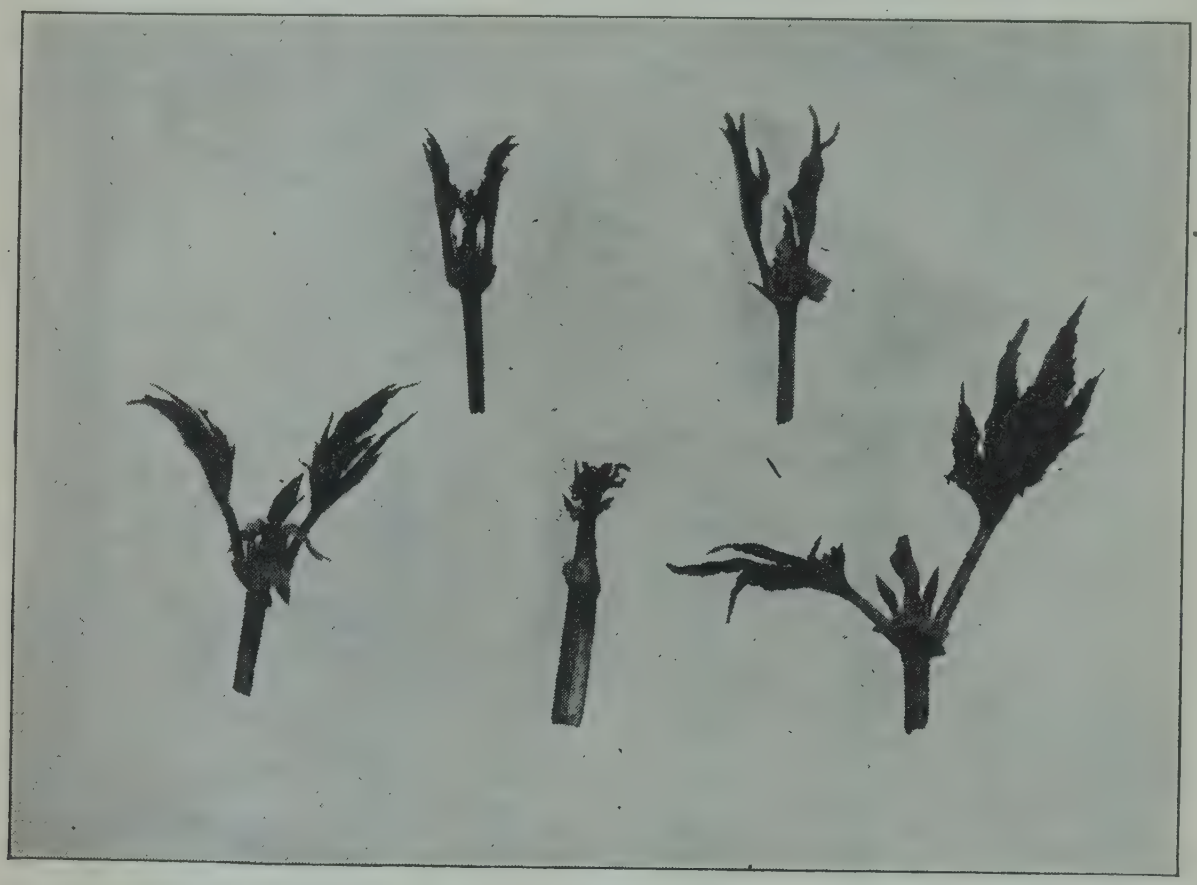

Fig. 11. MUFFLE-HEADED HOP VINES RESULTING FROM THE WORK OF THE HOP-VINE BORER. REDUCED

When the main bud is injured, the leaves and buds just below begin to develop

eggs, the heads of all the young shoots were completely riddled when early vines, then four feet up the poles, were free from injury. In 1915 larvae were found in the hop heads when the yards were first inspected on May 6. At that time the vines of the first lot were less than one foot high. Occasional muffle heads could still be found by the first of June. After working in the tip of the hop for from one to two weeks, most of the larvae drop to the ground and join those working in the vines.

The injury resulting from the work of the larva in the heads is relatively small. The men who tie the hops choose the unaffected vines, and if by accident a muffle-headed vine is used it may be replaced at the next tying. When the head is killed, the two buds at the node just beneath it will grow rapidly (fig. 11), and occasionally one of the arms thus resulting is twined on the pole in place of the main vine.

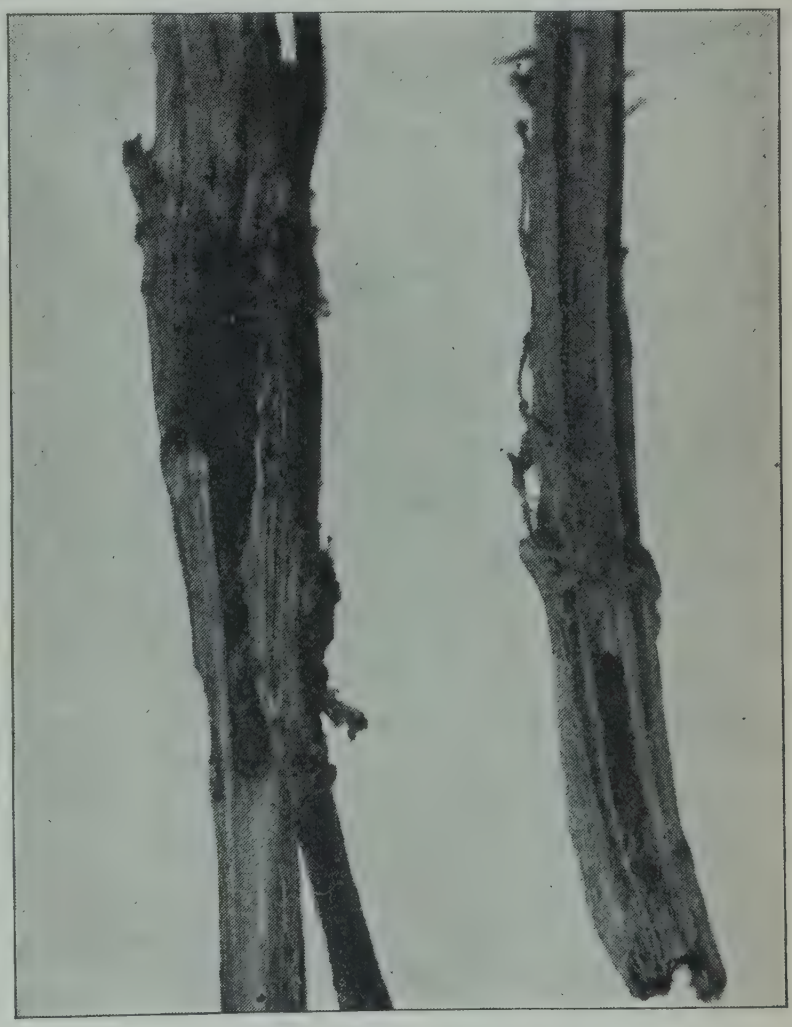

FIG. 12. VINES CUT OPEN TO SHOW THE WORK OF THE HOP-VINE BORER. $\times 1\frac{1}{2}$

*The early (inside) work in the vines*

In contradiction to earlier accounts, the writer has obtained evidence that many of the newly hatched larvae enter the hop vine at once, without first working in the hop heads. Most of the eggs hatch at a time when the vines are short and tender. The young larva enters usually near the surface of the ground — from two to four inches above the bed root. Only a small hole shows on the outside, but at this point the vine breaks on bending and the work of the young larva is found within. A discolored area running up or down the pithy center of the stem marks the course taken. The burrow is filled with waste material behind the little larva as it rapidly eats its way along (fig. 12). The larva grows, and sheds its skin at least twice before it is ready to eat its way from the vine, whose unyielding sides prevent further growth.

The newly hatched larva of *G. immanis* is less than 2 millimeters long, but when ready to leave the vines it has reached a length of from 8 to 18 millimeters. In 1915 most of the larvae were outside the vines by June 9. In the case of one hill examined on that date, one grub was in a hop vine, one was in a blade of grass on the hill, and seven were working on the outside of the vines.

While the larvae work oftener in young, tender shoots, they are sometimes found in the bases of vines that are well up the poles. Occasionally they enter a vine of this kind halfway to the tip, or from two to three feet above the ground. Sometimes a vine is found which has a muffle head and several larvae working in it at different points. All this strengthens the evidence that a larva, after crawling for some distance, enters wherever it can most easily make an opening.

When a larva leaves its burrow in the hop vine, it does one of two things: either it eats its way into a bed root, or it feeds on the outside of the vine between the bed root and the surface of the ground. In very rare cases larvae have been found feeding on runners, or rootstocks, which were not removed by grubbing in the spring.

*The late (outside) work on the vines*

After leaving the head of the hop or the inside of the vine, the larva usually attacks the outside of the vine and feeds on the sap that flows from the wound. In some cases the vine is eaten completely thru, but oftener it is held together by a small shred and enough nourishment passes thru to keep the foliage from wilting. After feeding in one place the larva often goes to another, above or below the old wound, and repeats its work. Vines thus attacked often send out extra rootlets above the wounded area, and much additional nourishment is received in this way. The sap is able to ascend in vines of this kind, but the return flow of manufactured food material to the roots is cut off. The vine swells above the injured area, due, no doubt, to the deposition of the material being carried downward. The roots, deprived of this food supply, become weaker and succumb more readily to the winter frosts. (Fig. 13.)

*The work in the roots*

Some of the larvae eat their way into the bed root on hatching, but it is commoner to find partly grown larvae in this position. Larvae

are especially abundant in the roots in unhilled yards, where the roots are close to the surface of the ground. Some grubs make shallow grooves on the outer surface, but many work in the core of the root in all directions. The writer has found twelve larvae in a single root. As the bed root is the part of a plant that lives over the winter and furnishes the growth for the coming season, any injury to it is a serious matter. One result of

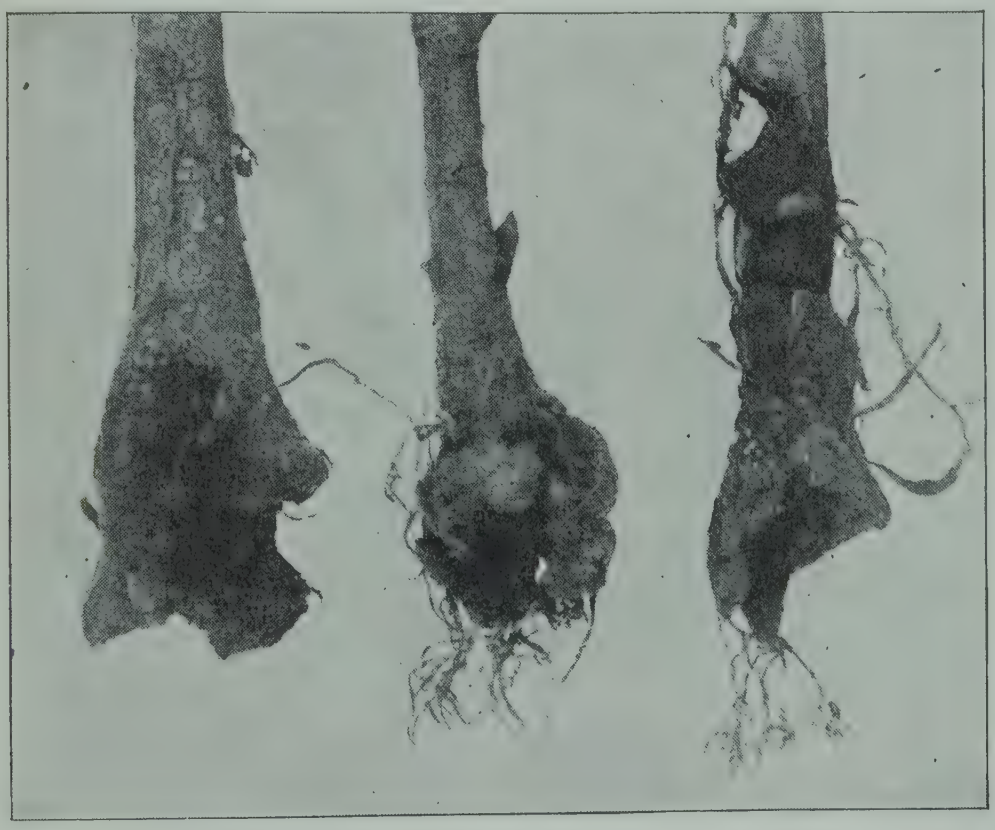

FIG. 13. VINES BROKEN OFF FROM THE BED ROOT AS A RESULT OF THE FEEDING OF THE HOP-VINE BORER. SLIGHTLY REDUCED

The enlargement above the place of attack is to be noted

this work of larvae is that an opening is made for soil water to seep in and freeze; also, fungi may enter and start decay. In yards that have been badly infested with grubs, as feeders on either vines or roots, the number of dead hills is always much greater the following spring.

Many grubs are working as external feeders or in the bed root by the end of the first week in June, and by the end of the second week nearly all have finished their work inside the vines. They mature and complete their work in the roots from the middle of July to the middle of August.

### THE WORK OF THE YOUNG LARVA IN GRASS

Early in the spring of 1915, larvae of *Gortyna immanis* were found working in grass plants in the hopyards (fig. 14). The work in grass is very similar to the early work in the hop vine. The grub enters, as a rule, close to the ground and bores upward thru the stem. Injured grass may soon be distinguished by the wilting of the central blade. The grub continues its work until about the third stage, and leaves the grass about the time the larvae are leaving the inside of the hop vines.

FIG. 14. LARVA OF HOP-VINE BORER IN A GRASS STEM. × 3

Early in the spring grass is common in many hopyards, giving the grubs a good place in which to start their growth (fig. 15). Many larvae are found in the grass along the borders of yards as well as in the yards themselves. It is probable that the moths go to the grass at the sides of the yards for shelter during the day, and lay their eggs there at night. After the eggs hatch, the larvae feed on the grass and later move to the hops. From this it is clear why the edges of the yards are often more seriously injured than the central parts. No larvae were found in grass at a distance from the yards.

In order to see whether other plants could act as hosts, weeds of all kinds were carefully examined, but in no case were larvae found working on them.

### TYPES OF YARDS ATTACKED

Poorly-cared-for hopyards having a growth of grass show more injury from *Gortyna immanis* than do those that are well cultivated (figs. 16 and 17). This may be due partly to the less vigorous growth in the former type of yard, but it may be attributed in large measure to the fact that the eggs of the insect are laid on grass and this grass furnishes

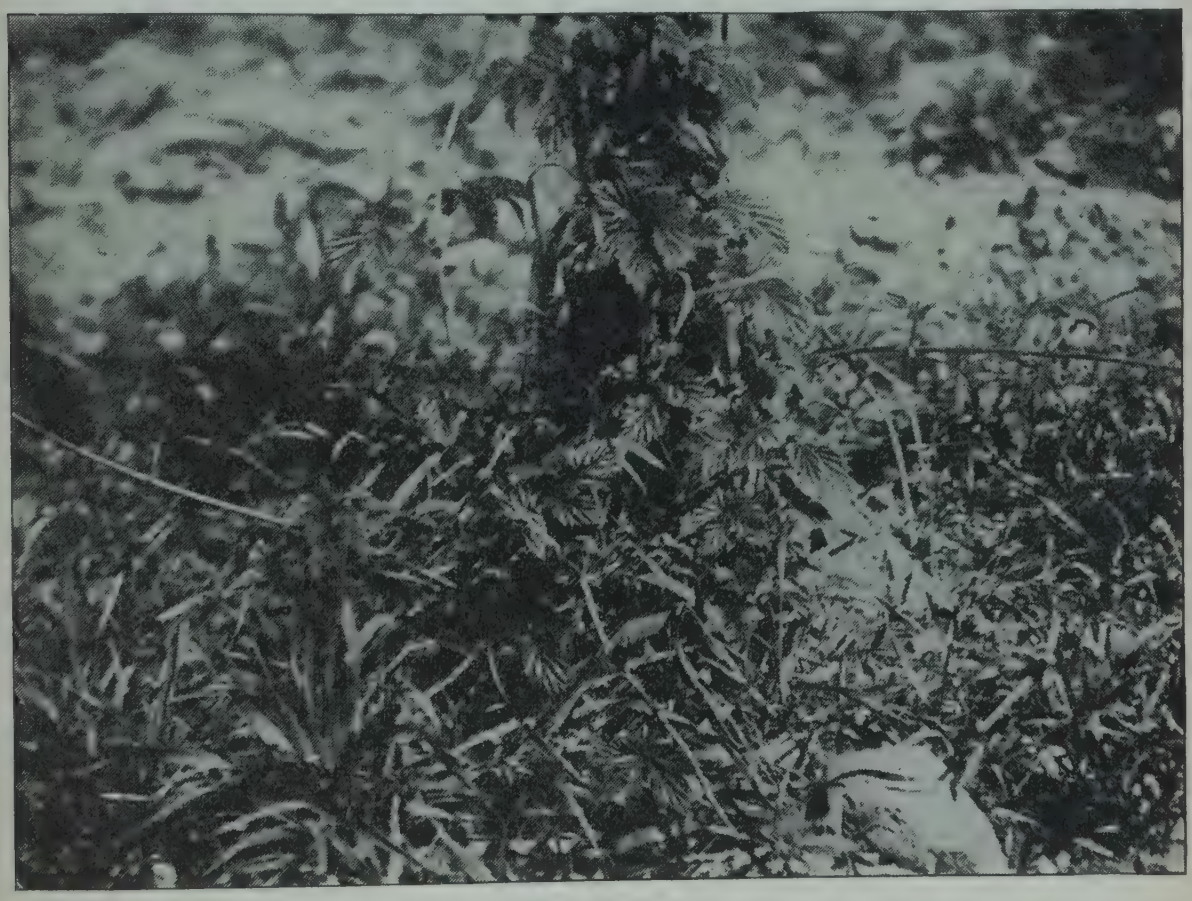

FIG. 15. GRASS AROUND A HOP HILL IN MAY
Many larvæ of *Gortyna immanis* work in grass at this time

food for many of the young larvae before they attack the hop. Yards newly set out, if near an infested yard, are often seriously damaged. One grower was compelled to reset a new yard four and five times in some places before he could get it successfully started.

Old yards in which the grubs have been allowed to work and multiply for a number of years, show the cumulative effect of such work. This is one reason given for taking up old yards and setting out new ones every five to ten years.

Fig. 16. A POORLY KEPT HOPYARD, IN WHICH HAVE BEEN FOUND MANY LARVAE OF THE HOP-VINE BORER

Fig. 17. A WELL-KEPT HOPYARD, IN WHICH BUT FEW LARVAE OF THE HOP-VINE BORER HAVE BEEN FOUND AT WORK

## DESCRIPTION OF THE SPECIES

### *The egg*

The egg of *Gortyna immanis* (fig. 18) is 0.65 millimeter in diameter and 0.43 millimeter thick, flattened above and below. The color of the egg when first laid is white or yellow-white, and turns to brownish pink in from one to three days. The egg is faintly marked on the side with about one hundred branching, radiating ridges. The micropyle end has a group of raised polygonal areas, with a rosette formation in the center.

FIG. 18. EGG OF HOP-VINE BORER. × 48

### *The larva*

The six stages thru which the larva passes may be described as follows:

*First stage.*— Length (collected specimen) 3 mm.; head 0.3 mm.; ground color dirty white, with prominent markings of old-rose red; sparse vestiture of setae. Head dark brown or black; antennae, ocelli, and mouth parts light yellow brown. Prothorax, anterior half dirty white, dorsal shield dark brown or black. Mesothorax with four rose-colored patches on lateral aspect of segments, forming a broad, broken, transverse band. Metathorax with markings similar to, but heavier and more irregular than, those of mesothorax. Thoracic legs with coxa white, femur, tibia, and tarsus brown. Abdomen with segments 1 to 8 banded similarly to mesothorax, but bands broader, covering nearly the entire segments; tubercles inconspicuous; spiracles small, dark-bordered, surrounded by a light ring; segment 9 more faintly marked; five pairs of prolegs; venter lighter but with rose tint on abdomen. In grass, hop heads, and vines.

(Only the prominent differences are noted in the descriptions following.)

*Second stage.*— Length 3.4–6.4 mm.; head 0.65 mm. (average of seven specimens); ground color more prominent, rose-colored markings often less extended and tending to orientation in longitudinal axis, on all segments of thorax and abdomen; setae about one-third as long as diameter of body, and tubercles bearing them more prominent. Head pale yellow-white, clypeus and labrum darker than other parts; ocelli in a dark patch; dark spot on dorsal shield divided by a median light line; spiracles larger, and especially prominent on prothorax. In grass, hop heads, and vines.

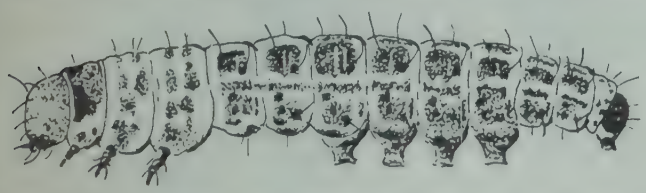

FIG. 19. LARVA OF HOP-VINE BORER, FOURTH STAGE. × 5

*Third stage.*— Length 6.8–8.4 mm.; head 1 mm. (average of eight specimens); ground color more extended and rose patches more regularly arranged; four longitudinal dark lines broken by light spaces; the second (subdorsal) line much narrower than the first and the third; tubercles bearing setae dark brown. In grass and vines.

*Fourth stage* (fig. 19).— Length 9-15 mm.; head 1.43 mm. (average of eight specimens); ground color still more extended; setae and tubercles large. In vines and in ground.

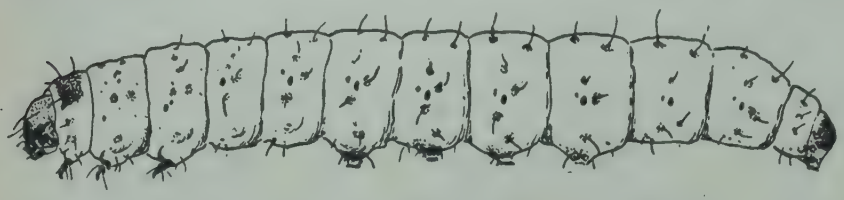

FIG. 20. LARVA OF HOP-VINE BORER, FULL-GROWN. × 1½

*Fifth stage.*— Length 17–25 mm.; head 2.22 mm. (average of eight specimens); rose markings faint in most specimens, in some entirely wanting. In ground or in roots.

*Sixth stage* (fig. 20).— Length 27–48 mm.; head 3.91 mm. (average of eight specimens); rose markings entirely lost; color dirty white; fat and unwieldy out of its burrow; tubercles bearing setae standing out prominently, as do brown marks on thoracic and anal shields. In ground.

## *The pupa*

The pupa (fig. 21) is from 20 to 28 millimeters in length and from 7 to 9 millimeters in diameter. It is usually dark brown, but in rare cases is lighter in tint. The cremaster consists of two short spines.

## *The adult*

The adult (fig. 22) is described as follows by Dr. W. T. M. Forbes:

The moth is light brown, with greenish or pinkish reflections in certain lights. The head and thorax are of the same color. The ordinary lines on the fore wing are slightly paler, nearly even, and defined on each side with a darker gray edging; the basal line is present; the t. a. line projects slightly at two points (on veins Sc and Cu); the inner boundary of the t. p., or the outer of the two principal lines, is sharply defined, but the outer is obscure; the line is bent at a right angle just below the costa, from which it starts at a small spot, is slightly bent out near the middle (at vein $M_2$), and is incurved below; the medial shade is single, dark, angled at the lower side of the cell, and waved below; the st. line (shortly before the margin) is irregular, especially above, and double toward the inner margin; there is a dark terminal

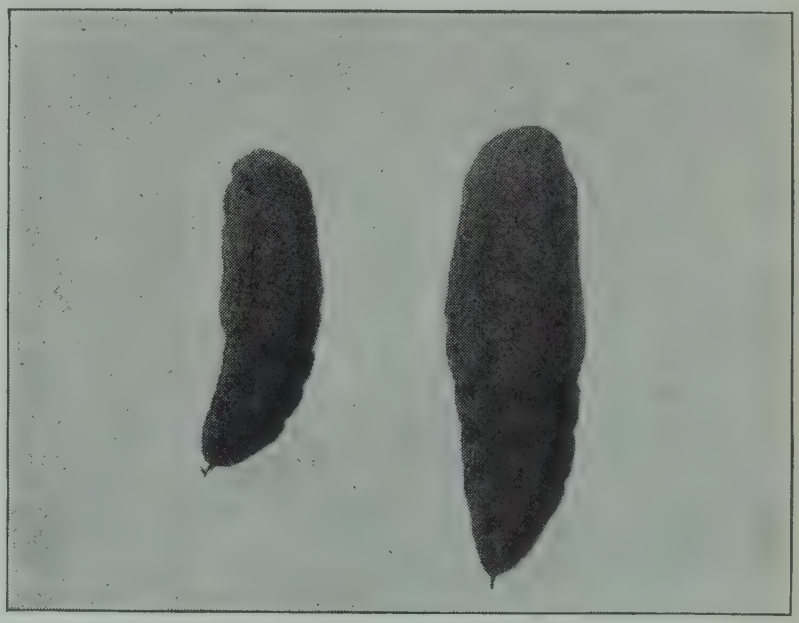

FIG. 21. PUPAE OF HOP-VINE BORER, SHOWING VARIATION IN SIZE. × 1½

line; the orbicular spot is erect, the reniform normal. The hind wing is grayer, with a somewhat pinkish fringe, dark veins, and an obscure pale and dark t. p. line. Female larger than male. Spread 40 to 51 mm.

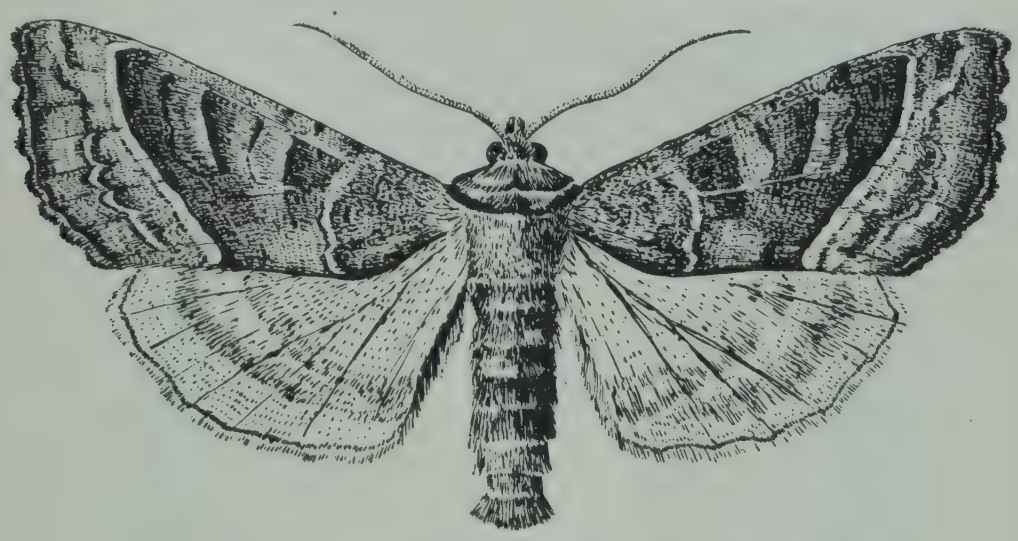

FIG. 22. ADULT FEMALE OF HOP-VINE BORER. × 2

## LIFE HISTORY AND HABITS

### *The egg*

The eggs of *Gortyna immanis* were said by Dodge (1882) and later writers to be laid on the tip of the hop vine by overwintering females, but the writer has never seen an egg in this position and has no evidence that they are ever so placed. Under field conditions eggs have been found only on grass, and here they have been found in large numbers.

Prior to 1915 eggs had been found deposited in various places in laboratory and field cages, but no eggs that were known to be those of *G. immanis* had been found under field conditions. In the spring of 1915 a search was made for eggs and young larvae, and on May 10 larvae were found working in grass stems and eggs were found on dead grass blades from the same root. In August of that year cages were built over hop hills on which grass was growing, and full-grown grubs and pupae were placed in them. On the grass in one cage eggs were found on September 1. They were laid both singly and in small groups. Most of the eggs were attached to the outer surface of the grass. On September 6 many eggs were found in the axils of the grass stems, in all cages. Several lots of eggs were found in the field near Sangerfield

on September 7, and from that time on there was little trouble in locating eggs on grass in any yard that had been infested by grubs. During 1915 eggs were found nowhere except on grass plants. (Figs 23 and 24.)

The egg stage lasts about eight months. Eggs are laid from the middle of August to the last of September, and hatch from the last week in April to the last of May. A distended female opened in 1914 contained 866 eggs. Others examined in 1915 had 725, 457, and 612 eggs, respectively. No data were gathered on eggs deposited. It is apparent that the number of eggs laid by a single moth may be large. Not all eggs hatch, as many turn black and shrivel soon after being laid. Both shriveled and healthy eggs are found in the same egg mass, and as many as fifty per cent may dry up — due, no doubt, to lack of fertilization.

Fig. 23. Eggs of hop-vine borer on a grass stem. × 3

Fig. 24. Eggs of hop-vine borer in a grass stem with the outer sheath removed. × 3

Eggs are laid soon after the moths emerge. The data for three individuals are given in table 1:

TABLE 1. LENGTH OF TIME BETWEEN EMERGENCE AND OVIPOSITION OF THREE MOTHS, 1915

| Date of emergence | First eggs laid | Days intervening |
|---|---|---|
| August 25 | September 2 | 8 |
| August 31 | September 5 | 5 |
| August 26 | September 6 | 11 |

*The larva*

In order to find the number of stages thru which the larva passes in its development, a series of head measurements were taken. Since the larva breeds in vines and beneath the surface of the ground, it is impossible to find the cast skins, and so grubs were preserved in alcohol during the summer of 1914. These were later examined and the transverse measure of the head was taken, as given in table 2:

TABLE 2. HEAD MEASUREMENTS OF LARVAE COLLECTED IN 1914

| Stage | Number of specimens | Diameter (in millimeters) | | |
|---|---|---|---|---|
| | | Greatest | Least | Average |
| 1st | 1 | 0.30 | 0.30 | 0.30 |
| 2d | 7 | 0.68 | 0.60 | 0.65 |
| 3d | 8 | 1.06 | 0.92 | 1.00 |
| 4th | 8 | 1.50 | 1.37 | 1.43 |
| 5th | 8 | 2.46 | 2.06 | 2.22 |
| 6th | 8 | 4.06 | 3.80 | 3.91 |

It is seen from the above data that the larva of *G. immanis* probably passes thru six stages with five molts. The entire length of the larval period is from nine to twelve weeks, since the young larvae hatch from the last of April to the middle of May and pupation occurs during July and the first half of August. No larvae have been successfully bred thru.

Smith (1884) reports that the larva makes a rude cell in which to pupate. Comstock (1883) did not observe this to be true. In rare cases

the writer has found a pupal cell. Whether or not one is formed depends on the texture and the moisture content of the soil at the time of pupation. If the soil is of the consistency of clay and is easily packed, a cell may be formed.

*The pupa.*

There is a wide variation in the size of pupae (fig. 21, page 160), as also in the size of adult moths. The writer believed that the small pupae must be those of males and that the large ones would develop into females. Breeding shows that this is not always true, since in some cases females have been reared from pupae of the smaller size.

In 1914 full-grown larvae of *G. immanis* were taken into an unheated field laboratory. The length of the pupal stage under these conditions was found to be as given in table 3:

TABLE 3. Length of Pupal Stage for Four Specimens under Laboratory Conditions

| Date of pupation | Date of emergence | Days intervening |
|---|---|---|
| July 2 | August 8 | 37 |
| July 3 | August 7 | 35 |
| July 5 | August 9 | 35 |
| July 6 | August 11 | 36 |

Average, 36 days.

From the above data it is seen that the pupal stage lasts a little over one month in the laboratory. Observations by the writer indicate that in the field it varies from four to six weeks. Pupation occurs in the field during July and in the first part of August, and moths emerge during August and September. In 1914 the first pupa was found on July 2, and in 1915 on July 9. In 1914 the first moth emerged on August 10, and in 1915 on August 11. At Waterville the writer found newly transformed moths in field cages as late as the middle of September.

In most cases the full-grown larva leaves the root or the vine and comes close to the surface of the ground before pupation. The pupa is often found some distance down the side of the hill — a foot from the place of larval feeding operations. In rare cases the pupa may be

found near the root and even beneath it. The moths on emerging often leave the pupal skin projecting above the ground. Smith (1884) reported that *G. immanis* usually winters in the pupal stage, but after three years of observation the writer is convinced that all pupae change to adults in the fall. Cages were examined late in September, and all healthy pupae had transformed.

FIG. 25. ADULT HOP-VINE BORER ON HOP POLE. SLIGHTLY REDUCED

### *The adult*

Adults of *G. immanis*, being colored much like dirt, dead leaves, and hop poles (fig. 25), are seldom seen in the field. It is not uncommon to search for moths in a cage for some time and then find them resting quietly a few inches away. If disturbed they usually flutter their wings and crawl a short distance, but do not fly far if at all.

After depositing eggs the moths die in a very short time, in most cases in about a week. In one case a moth lived for twelve days after completing oviposition. Sweetened solutions were placed in some cages, but did not greatly prolong life. These data were obtained by isolating moths the abdomens of which indicated that they had been laying eggs.

## SEASONAL HISTORY

The eggs of *Gortyna immanis* are laid in the fall on grass in and around hopyards. The eggs hatch the following spring, in April or May, and the young larvae make their way into grass or hop plants. In grass they eat into the stem near the surface of the ground and feed upward, killing the central blade. They leave the grass at about the time other larvae leave the inside of the hop.

In the hop the young grubs enter the part that is the most readily available and easy to penetrate. This may be the head or any part of the vine. If the larva enters the head, it drops to the ground in about two weeks and helps to increase the large number already working in the vine near the root. About the first of June, when the larva is in the third or the fourth stage, it stops inside work and either feeds on the outside of the vine, nearly or quite severing it, or makes burrows in the root. In July or the first part of August the larva pupates, and the moth emerges the last of August or early in September. The moth deposits eggs, which rest over the winter on grass. The moth dies soon after oviposition.

### RELATION OF CLIMATIC AND SOIL CONDITIONS TO SEASONAL HISTORY

Weather conditions have some influence on the life history of *Gortyna immanis*. A late, cold spring retards the development of the larvae somewhat, while warm weather hastens its growth. The winter of 1913–14 was attended with heavy snows which covered the ground in the hop country until late spring, while that of 1914–15 was open and the ground was not covered. A larger number of grubs were present the following spring under the former conditions, in a yard that was under close observation. The snow cover may act as a blanket for the overwintering eggs.

The larva works in any kind of soil. Yards on sandy soil, however, are less affected than those on gravel, clay, or loam.

### NATURAL ENEMIES

#### *Predatory enemies*

*The skunk.*— An important destroyer of the larvae, and probably of the pupae, of *Gortyna immanis*, is the skunk. About July 1, when the grubs have reached maturity, numerous holes may be seen in hop hills where skunks have been digging for the fat, juicy larvae. Sometimes the skunk digs the dirt entirely away from the bed root, leaving only about half of the hill standing (fig. 26); at other times it pushes the dirt aside with its nose, making a small, deep hole about three inches in diameter. Not every hill is attacked, and growers say that the animal, hearing the grub feeding, digs in only where it is sure its efforts will be rewarded. The skunk does not always find all the grubs that are present;

the writer has often taken both larvae and pupae from hills in which skunks had recently been working. It is seldom that the vines are injured by the work of the skunk, unless they have been badly eaten by the grub and are hanging by a mere shred.

As a control measure the skunk does much good by reducing the number of larvae and pupae that would complete their development. It does not, however, reduce the injury of the year, for by the time the skunk becomes active the larvae are full-grown and the damage is done.

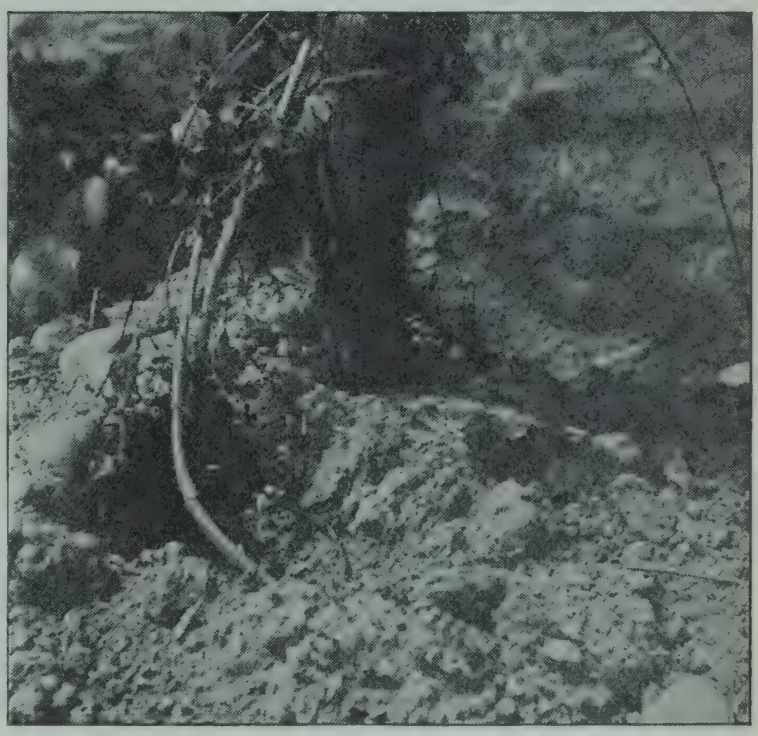

FIG. 26. A HOP HILL SHOWING THE HOLE MADE BY A SKUNK IN DIGGING FOR THE LARVAE OF THE HOP-VINE BORER

*Predacious beetles.*—Several species of carabids feed on the larvae of *G. immanis*, the most daring of these being *Calosoma calidum* Fab. Both the larva and the adult of this species (figs. 27 and 28) are active in attacking the grubs of *G. immanis*. The adults, at least, of other smaller carabids feed on the larvae of *G. immanis* in the younger stages. The following species are known to be predacious: *Harpalus pennsylvanicus* Dej.; *Pterostichus lucublandus* Say; *Pterostichus stygicus* Say; *Amara impuncticollis* Say.

In breeding cages the writer has found dead pupae and adults with holes eaten in the sides of the abdomen. Carabids found in the cages are believed to have done this work. A small carabid collected in the field and placed in a bottle containing several pupae had destroyed one before the laboratory was reached. Masses of eggs partially eaten by a predatory enemy have also been found, and carabids were present in the cage at that time.

*Parasites*

*Hymenopterous parasites.*— The braconid *Microplitis gortynae* Riley[3] is a common parasite on the larva of *Gortyna immanis.* In 1914 the writer found large numbers of braconid cocoons close to depleted larval skins of the grubs. Eighty cocoons were found with a single skin. These were kept over winter but adults did not emerge. On June 11, 1915, the writer found more of the cocoons when digging grubs. Some adults had emerged and more were just coming out at the time. The braconids were found on top of the ground and crawling all thru the dirt. Some specimens taken to the laboratory and placed with partly grown larvae began laying eggs at once. One larva, when attacked, whipped its body back and forth, crawled between pieces of dirt, and even turned completely over. In spite of these efforts the parasite still clung firmly until its object was accomplished.

FIG. 27. LARVA OF PREDACIOUS BEETLE. ABOUT NATURAL SIZE
*Calosoma calidum*

FIG. 28. ADULT OF PREDACIOUS BEETLE. SLIGHTLY ENLARGED
*Calosoma calidum*

For two weeks after the observation just recorded, braconids were often seen crawling in search of a host in the infested hopyards about Waterville; and later in the summer the cocoons were again found, both in cages and in the field. The larva of the parasite apparently leaves the grub just as the latter is about to pupate. A cocoon of a braconid parasite was found with a dead grub on July 9; a specimen belonging to the genus *Aenoplex*[3] emerged from this on August 15. Chalcid parasites (*Synaldis* sp.) were bred on August 10 from grubs found on July 9.

[3] Determined by A. B. Gahan thru the kindness of Dr. L. O. Howard.

*Dipterous parasites.*— In the summer of 1914 a tachinid fly, *Frontina frenchii* Will.,[4] was reared from a full-grown larva. On June 12, 1915, in examining work in vines, a grub skin of *Gortyna immanis* was found with many dipterous larvae crawling in it. Dr. O. A. Johannsen has identified adults bred from these larvae as *Masicera myoidea* Desvoidy, also a tachinid.

*Fungous parasites.*— In both 1913 and 1914 dead grubs were found which were covered with a fungous growth. In the spring of 1914, F. M. Blodgett succeeded in obtaining from one of these a culture of what appeared to be *Sporotrichum globuliferum.* Later spore suspensions of this fungus were injected into hop hills, but no indication of its inoculating the grubs could be found.

## CONTROL

The control of *Gortyna immanis* as practiced in the hopyards of New York State has been almost entirely based on cultural measures. Pinching the tips of the hops that were muffle-headed has been recommended (Dodge, 1882, and later writers), but since few larvae enter the heads this alone is insufficient. Another control method suggested (Dodge, 1882, and others) is to dig the dirt away from the vines and the roots in spring, and leave them in this condition until late in July or early in August, at which time, it is advised, a composite consisting of equal parts of salt, quicklime, and hen manure should be added. It was believed that under these conditions the vines would become so tough that the grubs could not injure them. So far as the writer knows, this method is not practiced at the present time.

In order to test the effect of leaving the roots uncovered, as suggested above, the dirt was removed from ten hills in two yards about June 1. When one yard was examined later, the vines in these ten hills were found to be less developed than the vines in adjacent hills. There were no grubs in this yard. In the other yard grubs were found working in both the vines and the bed roots.

Still another method of control that has been recommended (Dodge, 1882, and other writers) is high hilling. In hilling, men throw dirt around the vines with shovels, covering the hill several inches deep, or plow

[4] Determined by J. D. Tothill.

close to the hill turning a furrow over it. This is done in June or early July. Some growers claim that hilling draws the grub to the surface and away from its place of feeding on the vine. The writer has not found this to be true. In several yards hilled very high, grubs have been found in quantities in and around the bed root — a foot or more below the surface of the ground.

In highly hilled, well-fertilized yards, the vines often send out rootlets above the injured areas. These supply nourishment to so large an extent that vines nearly severed are often kept alive by this means. Hilling is a good practice for this reason if for no other.

A hop root sends up many more vines than are needed for cultural purposes. When the hops are tied the second time, which is usually about June 1, these extra vines are pulled up or cut off with a knife. This practice is of use in grub control if done in the right manner. At this time many of the grubs are working on the inside of the vines, and if the vines are destroyed the grubs will be killed. It is better to pull the vines out than to cut them off, for, if larvae are working in the vines near the crown, the cut may come above them and they are then free to crawl out and enter vines that have been twined on the poles. The writer has seen many grubs in the stumps of the vines just below the place where they were cut off, and has observed them crawling to adjacent plants. If the vines are pulled, they break off where they join the root. All sprouted vines should be taken from the yards. As grubs work in the late shoots just coming above the ground, these also should be removed at this time. In 1915 most of the grubs were outside the vines by June 9, and the practice of sprouting, to be effective, should in ordinary years be completed before June 1.

An old recommendation (Smith, 1884) is to place wood ashes around vines or scatter them on top of the hills. In 1914 one grower did this about June 13. On examining that yard some time later, the writer found live grubs to be numerous in every hill and dead vines were unusually plentiful.

Sometimes growers resort to digging out the larvae. This has been done in early June, when the work outside the vines was just beginning. The soil is removed from around the hills down to the bed root with a hoe, and the dirt is worked away from between the vines with a pointed stick

in order to remove any grubs that may be feeding deep down near the roots. William Durar, working for George Allen, a grower, at Sangerfield, New York, found that it took twenty-eight hours to go over 267 hills. He averaged, therefore, between 9 and 10 hills an hour, but in addition to digging out the grubs he removed the dead vines and trimmed off the lower arms. If all the time had been spent in digging grubs, it is probable that 12 hills an hour could have been gone over, or 120 hills in a day. At this rate it would take about six days for one man to dig one acre, amounting, at $2 a day, to $12 an acre. Another grower reports that grubs can be dug at the rate of 200 hills a day — a cost of $7.50 an acre. This makes digging a rather expensive process.

In digging grubs, vines that are weakened by feeding may be broken off, and in ordinary practice of this kind the larvae working in the roots would not be found. Men in the hop sections are needed for other work at this season of the year, and it is difficult to get help that can be relied on to do this work in a proper manner. For these reasons, the writer undertook a series of experiments to see whether an effective method of control could not be found at a more reasonable cost to the grower and with less demand on greatly needed labor. The results of these experiments are given in the following pages.

### *Experiments in 1914*

Most of the experiments in 1914 were conducted in the Gallagher yard at Sangerfield, New York. The soil in this yard is a gravelly loam. At the time when most of the materials were applied, the soil was mellow and slightly moist and phosphate had been added at the rate of a few handfuls to each hill. Experiments were conducted in several parts of the yard at once, and counts were made from several hills in each of these plots.

The test of efficiency for most materials is that few live grubs are to be found in the hills when counted. The number of grubs to the hill varies greatly, and so a count of a small number of hills may not give a true average; it may be said, however, that in any case when three or more grubs are left alive, the material may be considered ineffective, as three grubs can destroy an entire hill.

The results of the experiments conducted in 1914 are given in table 4:

TABLE 4. RESULTS OF EXPERIMENTS IN THE GALLAGHER YARD IN 1914

| Experiment | Material used | Date of application | Date when grubs were counted | Amount of material applied to each hill | Place of application | Number of hills counted | Number of grubs to a hill | Remarks |
|---|---|---|---|---|---|---|---|---|
| C..... | Tobacco dust | May 25 | June 25 | 1 handful | In and on hills | 10 | 4.6 | |
| D..... | Tobacco dust and sulfur | May 25 | June 25 | 1 handful | In and on hills | 8 | 7.0 | Equal parts |
| E..... | Tobacco dust and lime | May 23 | June 26 | 1 handful | In and on hills | 8 | 8.1 | Equal parts |
| H..... | Cornell (Lawry) insect powder with sulfur | May 24 | June 23 | 1 handful | In hills | 10 | 5.3 | Vines burned |
| I..... | Oil of tansy and lime | May 23 | June 23 | 1 handful | In hills | 10 | 8.6 | 1 ounce of oil of tansy mixed with 12½ pounds of lime and 1 pint of wood alcohol |
| J..... | Hellebore and lime | May 24 | June 23 | 1 and 2 handfuls | In hills | 10 | 7.8 | 1–4 |
| K..... | Carbolic acid emulsion, no. 1 | May 25 | June 25 | About 1 pint | On hills | 10 | 4.9 | Vines discolored |
| L..... | Hellebore decoction | May 24 | June 23 | About 1 pint | On hills | 10 | 7.9 | 5 ounces of hellebore, 2½ quarts of water, diluted to 2½ gallons |
| M..... | Arsenate of lead and sulfur | May 23 | June 26 | 1 handful | In and on hills | 10 | 7.5 | 1–4 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| N..... | Arsenate of lead—vine spray | May 24 | June 20 | About 1 pint | On hills | 10 | 8.3 | 5 pounds to 50 gallons of water |
| S..... | Salt solution (saturated) | July 2 | July 3 | 3 quarts | On hills | 4 | 9.0 | All vines killed |
| U..... | Kerosene emulsion (15 per cent) | June 11 | June 13 | Drench | On hills | 5 | 6.0 | |
| V..... | Black-leaf-40 | June 11 | June 13 | Drench | On hills | 10 | 3.0 | 1–400, with soap 10–50 |
| W..... | Carbolic acid emulsion, no. 2 | June 11 | June 18 | Drench | On hills | 5 | 9.6 | 500 cc. of water, 1000 cc. of acid, 2 ounces of soap diluted to 2½ gallons |
| X..... | Check | ..... | ..... | ..... | ..... | 20 | 8.3 | |

*Experiments with carbon disulfid*

Carbon disulfid was tried as a control measure against the larvae in the Gallagher yard. In the first experiment, on July 2, a hole was made in the soil with a sharpened stick and the liquid was poured into it from a bottle. The hole was then filled in. A pint of material was used in eight hills. One hill was opened in fifteen minutes and the remainder

TABLE 5. RESULTS OF EXPERIMENTS WITH CARBON DISULFID IN 1914 — SERIES I
(Time between injection and examination, from 48 to 50 hours. No injury to vines)

| Experiment | Distance of application from root (inches) | Number of injections | Quantity used in each injection (cubic centimeters) | Depth of injection (inches) | Number of grubs found | Depth of grubs when found (inches) | Condition of grubs |
|---|---|---|---|---|---|---|---|
| 21 | 3 | 1 | 4 | 6 | 2 | 3 | Sick |
| 22 | 3 | 1 | 8 | 6 | 1 | 3 | Dead |
| 23 | 3 | 2 | 2 | 6 | 2 | 2 | Alive, sick |
| 24 | 3 | 2 | 4 | 6 | 1 | 5 | Dead |
| 25 | 6 | 1 | 2 | 6 | 1 | 3 | Dead |
| 26 | 6 | 1 | 4 | 6 | 2 | 4 | Dead |
| 27 | 6 | 1 | 8 | 6 | 1 | 4 | Dead |
| 28 | 6 | 2 | 2 | 6 | 1 | 6 | Dead |
| 29 | 6 | 2 | 4 | 6 | 1 | 5 | Dead |
| 30 | 6 | 2 | 8 | 6 | 2 | 4 | Dead |
| 32 | 12 | 1 | 4 | 6 | 1 | 3 | Alive, active |
| 33 | 12 | 1 | 8 | 6 | 2 | 5<br>7 | Dead<br>Nearly dead |
| 34 | 12 | 2 | 2 | 6 | 1 | 4 | Sick |
| 35 | 12 | 2 | 4 | 6 | 1 | 3 | Alive |

TABLE 6. RESULTS OF EXPERIMENTS WITH CARBON DISULFID IN 1914 — SERIES II
(Time between injection and examination, from 48 to 54 hours. No injury to vines)

| Experiment | Distance of application from root (inches) | Number of injections | Quantity used in each injection (cubic centimeters) | Depth of injection (inches) | Number of grubs found | Depth of grubs when found (inches) | Condition of grubs |
|---|---|---|---|---|---|---|---|
| 20 | 3 | 1 | 2 | 6 | 1 | 3 | Dead |
| 21 | 3 | 1 | 4 | 6 | 1 | 4 | Dead |
| 22 | 3 | 1 | 8 | 6 | 1 | 3 | Dead |
| 23 | 3 | 2 | 2 | 6 | 1 | 5 | Dead |
| 24 | 3 | 2 | 4 | 6 | 1 | 4 | Dead |
| 25 | | | | | | | |
| 1 | 6 | 1 | 2 | 6 | 1 | 4 | Dead |
| 2 | 6 | 1 | 2 | 6 | 1 | 3 | Dead |
| 3 | 6 | 1 | 2 | 6 | 1 | 2 | Dead |
| 26 | | | | | | | |
| 1 | 6 | 1 | 4 | 6 | 1 | 2 | Alive, sick |
| 2 | 6 | 1 | 4 | 6 | 1 | 4 | Dead |
| 3 | 6 | 1 | 4 | 6 | 1 | 6 | Dead |
| 27 | | | | | | | |
| 1 | 6 | 1 | 8 | 6 | 1 | 3 | Dead |
| 2 | 6 | 1 | 8 | 6 | 1 | 2 | Dead |
| 3 | 6 | 1 | 8 | 6 | 1 | 5 | Dead |
| 28 | | | | | | | |
| 1 | 6 | 2 | 2 | 6 | 1 | 2 | Sick |
| 2 | 6 | 2 | 2 | 6 | 1 | 7 | Dead |
| 29 | | | | | | | |
| 1 | 6 | 2 | 4 | 6 | 1 | 3 | Sick |
| 2 | 6 | 2 | 4 | 6 | 1 | 5 | Dead |
| 30 | 6 | 2 | 8 | 6 | 1 | 4 | Dead |

in from one and one-half to two hours. Two grubs in the first hill opened recovered from the effects of the vapor, but 57 in the other seven hills were all dead. Many vines were injured. On the following day one pint of the material was applied to twenty hills. From four to seven hours

after the treatment, 118 grubs were found; of these, 106 were dead, 6 were dying, and 6 were alive. The live grubs were on the opposite side of the pole from the injection, or on runners at some distance from the root. The vines in some of the hills were killed.

Conditions at this time were favorable for the effective working of the vapor. The soil was slightly moist and was mellow, and the yard was hilled high. In addition to the grubs, millipedes and bettle larvae were killed. By this time the larvae were full-grown and were becoming scarce. A few were found, however, and these were placed in the center of the hills and doses of different strengths were tried against them. The results are shown in tables 5 and 6 (pages 174 and 175). From these tables it is seen that, under ideal conditions, doses as low as two cubic centimeters to a hill were found effective. Of all the materials tried in 1914, carbon disulfid alone showed signs of success, and therefore the writer decided to test the material more fully in 1915.

In order to test the effect of carbon disulfid on the hops, another series of experiments was conducted. The more important results are given in table 7:

TABLE 7. RESULTS OF INJURY EXPERIMENTS WITH CARBON DISULFID IN 1914

| Experiment | Distance of application from root | Number of injections | Quantity used in each injection (cubic centimeters) | Depth of injection (inches) | Resulting injury to plant |
|---|---|---|---|---|---|
| 1 | Next to root | 1 | 8 | 6 | 2 dead vines |
| 2 | Next to root | 1 | 4 | 6 | None |
| 3 | 6 inches | 1 | 16 | 6 | None |
| 4 | 6 inches | 1 | 16 | 6 | None |
| 5 | 6 inches | 1 | 16 | 6 | None |
| 6 | 6 inches | 1 | 16 | 6 | None |
| 7 | 6 inches | 1 | 16 | 6 | None |
| 8 | 6 inches | 1 | 16 | 6 | None |

## *Experiments in 1915*

### *Experiments with carbon disulfid*

In the spring of 1915, the writer again started experiments with carbon disulfid. These included investigation not only of its use in grub control, but also of the resulting injury to hop plants. The results are given in table 8:

TABLE 8. RESULTS OF CARBON DISULFID INJECTION EXPERIMENTS IN 1915

| Experiment | Yard | Quantity used in each injection (cubic centimeters) | Number of injections | Rainfall during experiment (inches) | Date of injection | Date when grubs were counted | Number of hills | Larvae found | | | | | | Number of hills in check | Number of grubs to a hill in check |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Total number | Number dead | Number sick | Number alive | Per cent dead | Number alive to a hill | | |
| A | Gallagher | 10 | 1 | 0.05 | June 9 | June 11 | 8 | 16 | 6 | 2 | 8 | 37 | 1.2 | 25 | 1.7 |
| B | Gallagher | 2 | 1 | 1.21 | June 16 | June 18 | 10 | 9 | 3 | 2 | 4 | 33 | 0.6 | 25 | 1.7 |
| C 3 | Gallagher | 10 | 1 | 1.21 | June 16 | June 18 | 10 | 13 | 6 | 5 | 2 | 46 | 0.7 | 25 | 1.7 |
| 4 | Gallagher | 5 | 2 | 1.21 | June 16 | June 18 | 10 | 9 | 6 | 0 | 3 | 67 | 0.3 | 25 | 1.7 |
| 2 | Gallagher | 4 | 1 | 1.21 | June 16 | June 18 | 10 | 20 | 6 | 2 | 12 | 30 | 1.4 | 25 | 1.7 |
| 1 | Gallagher | 2 | 2 | 1.21 | June 16 | June 18 | 10 | 16 | 7 | 6 | 3 | 44 | 0.9 | 25 | 1.7 |
| B 2 | Hicks | 5 | 1 | 1.66 | June 21 | June 25 | 10 | 13 | 3 | 1 | 9 | 23 | 1.0 | 20 | 4.2 |
| 4 | Hicks | 15 | 1 | 1.66 | June 21 | June 25 | 10 | 19 | 15 | 3 | 1 | 79 | 0.4 | 20 | 4.2 |
| C 4 | Hicks | 5 | 2 | 1.66 | June 21 | June 25 | 10 | 73 | 41 | 9 | 23 | 56 | 3.2 | 20 | 4.2 |
| D 1 | Hicks | 5 | 1 | 1.66 | June 21 | June 25 | 10 | 21 | 12 | 3 | 6 | 57 | 0.9 | 20 | 4.2 |
| 2 | Hicks | 10 | 1 | 1.66 | June 21 | June 25 | 10 | 28 | 17 | 0 | 11 | 61 | 1.1 | 20 | 4.2 |
| B 3 | Hovey | 10 | 1 | 1.8 | June 21 | June 28 | 10 | 23 | 12 | 4 | 7 | 52 | 1.1 | 20 | 1.8 |
| C 4 | Hovey | 5 | 2 | 1.8 | June 21 | June 28 | 10 | 17 | 4 | 3 | 10 | 23 | 1.3 | 20 | 1.8 |
| B 2 | Hovey | 5 | 1 | 1.8 | June 21 | June 28 | 10 | 13 | 3 | 1 | 9 | 23 | 1.0 | 20 | 1.8 |
| 1 | Locke | 5 | 1 | 2.1 | June 11 | June 22 | 12 | 23 | 0 | 0 | 23 | 0 | 1.9 | 6 | 3.8 |
| 2 | Locke | 5 | 1 | 4.87 | June 22 | July 7 | 8 | 15 | 4 | 0 | 11 | 27 | 1.4 | 8 | 10.5 |
| 3 | Locke | 5 | 2 | 4.87 | June 22 | July 7 | 8 | 16 | 1 | 2 | 13 | 6 | 1.9 | 8 | 10.5 |
| | Louie | 10 | 1 | 4.36 | June 22 | July 2 | 10 | 90 | 18 | 0 | 72 | 20 | 7.2 | .... | ..... |
| | Thayer | 10 | 1 | 3.96 | June 23 | July 7 | 10 | 22 | 0 | 0 | 22 | 0 | 2.2 | 5 | 3.0 |
| | Campbell | 15 | 1 | 3.21 | June 24 | July 7 | 5 | 4 | 0 | 0 | 4 | 0 | 0.8 | 5 | 5.0 |
| | Auger | 5 | 1 | 2.73 | June 12 | June 23 | 5 | 56 | 6 | 0 | 50 | 11 | 10.0 | .... | ..... |
| | King | 5 | 1 | 2.73 | June 12 | June 23 | 5 | 34 | 0 | 0 | 34 | 0 | 6.8 | 5 | 6.4 |
| | Moakler | 5 | 1 | 3.21 | June 24 | July 7 | 5 | 33 | 0 | 0 | 33 | 0 | 6.6 | 3 | 12.3 |
| | Walradt | 5 | 1 | 3.21 | June 24 | July 7 | 6 | 16 | 0 | 0 | 16 | 0 | 2.7 | .... | 2.5 |
| | Walradt | 5 | 1 | 3.21 | June 24 | July 7 | 6 | 12 | 0 | 0 | 12 | 0 | 2.0 | 3 | 2.5 |
| | Total | ..... | ..... | ..... | ..... | ..... | 218 | 611 | 170 | 43 | 398 | .... | .... | .... | ..... |
| | Average | ..... | ..... | ..... | ..... | ..... | .... | .... | .... | .... | .... | 27.8 | 1.8 | .... | 3.5 |

In conducting the experiments recorded above, the writer had to contend with a serious handicap in the way of frequent and heavy rains. Much of the soil in the hop region has some clay in its composition. When moist, a soil of this nature is so compact that the vapor meets an impassable barrier. With injections as far as six inches from the vines, it was found that the carbon disulfid was ineffective. Increasing the dose did not give better results. As a last resort injections near the plants, in most cases directly above the roots, were tried. The result in this case was still ineffective in controlling the grubs and in many cases was disastrous to the plants. In the experiments recorded in table 8, vines were killed as follows: Hicks, B 2, one vine; B 4, four vines; D 2, three vines; Hovey, B 3, many vines; Thayer, fifteen vines; Campbell, nine vines; Moakler, six vines; Walradt, many vines. The depth of injections was from two to three inches.

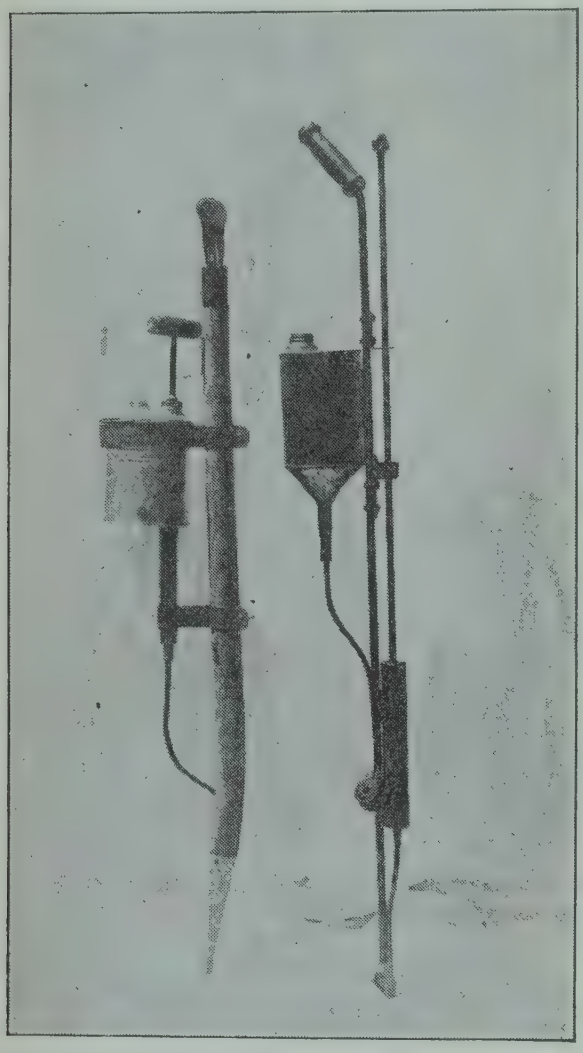

Fig. 29. Two types of injectors for use in treating soil with carbon disulfid

With the object of finding a way to place the liquid rapidly and uniformly in the soil, the writer, with the aid of F. M. Blodgett, devised an injector (fig. 29). So far as the writer knows, nothing of the kind is at present on the market in this country.

From the data in table 8, it is seen that the counts of living and of dead grubs show only 27.8 per cent control for the season's work. Sick grubs in the counts are considered as live ones because, due to the length of time and the weakening of the vapor density between injection and counting, sick ones would no doubt have recovered. The average number of live grubs per hill is given to show the comparative averages for check and for treated plots.

Taken as a whole, the results are very unsatisfactory. The writer believes, however, that in some soil and under ideal moisture conditions good results may be obtained. Since these conditions cannot be controlled the use of carbon disulfid is of doubtful importance.

*Injury to hop vines from carbon disulfid.*— Carbon disulfid will kill a hop vine or root whenever it comes into actual contact with it. The writer has noticed that vines which are badly eaten by the grubs are killed oftener than those that are not. A series of experiments in moist sandy soil showed that 15 cubic centimeters of carbon disulfid placed close to the vines had no serious effect. The sandy soil, being porous, no doubt allowed a better spread of the vapor. The results of an experiment in the Gallagher yard, where the soil is a gravelly loam, are given in table 9:

TABLE 9. RESULTS OF INJURY EXPERIMENTS WITH CARBON DISULFID IN 1915

(Injections were made on June 16; plants were examined on July 10)

| Experiment | Quantity used in each injection (cubic centimeters) | Number of injections | Distance of application from root (inches) | Number of live vines | Number of dead vines |
|---|---|---|---|---|---|
| 1 a | 16 | 1 | 4 | 2 | 2 |
| 1 b | 8 | 2 | 4 | 4 | 0 |
| 2 a | 24 | 1 | 4 | 2 | 2 |
| 2 b | 12 | 2 | 4 | 2 | 2 |
| 3 a | 32 | 1 | 4 | 0 | 4 |
| 3 b | 16 | 2 | 4 | 0 | 4 |
| 4 b | 21 | 2 | 4 | 0 | 4 |
| 5 b | 24 | 2 | 4 | 1 | 3 |

*Experiments with poison bait*

In spite of poor results obtained in 1914 from the use of poison bait it seemed possible that it might be applied successfully, and on June 11, 1915, a plot in the Gallagher yard was treated with a bait composed of $2\frac{1}{2}$ pounds of bran, $\frac{1}{2}$ pound of white arsenic, $1\frac{1}{2}$ pint of molasses, and the juice of an orange. This is stronger in arsenic than the mixture used against the army worm.

A rainfall of 0.26 inch occurred soon after this experiment was started, and therefore another plot was treated on June 12 with a mixture of the same strength. The material was placed close around the vines, the dirt

being removed to make this possible. On June 14 the following counts were made: in the plot treated on June 11 there were 30 grubs in ten hills, of which 28 were alive and 2 were dead; in the plot treated on June 12 there were 27 grubs in ten hills, all of which were alive; the check showed 29 grubs in ten hills. Grubs placed in a jelly glass with poison bait on June 12 were sick on June 13 and died on June 14. It is probable, therefore, that these larvae will feed on poison bait when the preferred hop vines are not present, but that they will not touch it under field conditions. A bait applied in May to catch the hatching larvae might prove effective.

*Experiments with para-dichlorobenzene*

Para-dichlorobenzene has been successfully used against various pests of stored grains. Duckett (1915) described its use, and from his account the following data are taken: Para-dichlorobenzene is a colorless, crystalline substance with a boiling point of 341.6° F. It volatilizes readily as a colorless vapor with an ether-like odor. This vapor, which is five times as heavy as air and twice as heavy as carbon disulfid vapor, is harmless to human beings but is a specific poison for insects under many conditions, killing by action on the nervous system. The insect begins quivering and finally turns on its back and, still quivering, dies. The cost is 15 cents a pound in barrel lots, and 35 cents a pound in small quantities.

It may be added that in 1915, due to the war, the price of para-dichlorobenzene rose to 35 cents a pound in large lots and 60 cents a pound in small quantities, and it was soon impossible to obtain it at these prices. However, it is now manufactured in this country and may be obtained at a much lower cost. So far as published results indicate, its use is recommended only in the case of certain stored-grain and household insects.

The writer tested this material against the larva of *Gortyna immanis*. The results of three experiments are given in table 10.

In all cases the characteristic odor was noticeable and crystals could still be found in the hills when they were examined. Of the seven live grubs in the Hicks yard, two were near the surface and three were on runners at some distance to one side. Sick grubs were counted as dead, since the material was still active and would doubtless have killed them if left undisturbed. Dead Lachnosterna larvae and carabids also were found, but millipedes were usually able to escape the action of the vapor.

Dead grubs are soft and black, and sick grubs are often slightly discolored. The vapor would no doubt spread more rapidly in normal years, free from the frequent heavy rains, and it will be interesting to see the effect of the material on the grubs under ordinary conditions. No plant injury was noticed during the experiments, but 56 grams of para-dichlorobenzene placed around one hill killed the plant in eleven days.

TABLE 10. RESULTS OF EXPERIMENTS WITH PARA-DICHLOROBENZENE
(Ten hills counted in each yard)

| Yard | Date when experiment was started | Date when experiment was closed | Amount of material used | Larvae found | | | | Per cent of control |
|---|---|---|---|---|---|---|---|---|
| | | | | Total number | Number dead | Number sick | Number alive | |
| Gallagher | June 18 | July 10 | A few crystals | 14 | 12 | 1 | 1 | 92.8 |
| Hicks | June 21 | July 10 | A few crystals | 39 | 28 | 4 | 7 | 82.0 |
| Hovey | June 21 | June 28 | A few crystals | 37 | 32 | 3 | 2 | 94.6 |

The ideal insecticide for grub control would be a material with long-lasting effect, which could be easily placed in the soil when early hilling is practiced. Para-dichlorobenzene may act successfully in this way. Its insolubility in water and its activity in the soil over such long periods of time would tend to indicate this. More study should be given to this side of the work.

*Recommendations*

The following practices are recommended for control of the hop-vine borer:

1. Remove all extra vines before June 1. Pull out the extra vines and remove them some distance from the yard.
2. Hill the hops, so as to give the extra rootlets an opportunity to grow.
3. Practice clean cultivation; in other words, remove the grass from the yard.
4. Keep a plowed border several yards wide around the field.
5. For an insecticide, experiment with para-dichlorobenzene, using a few crystals in each hill and covering with about two inches of dirt. This should be applied about the third week of May.

## THE HOP REDBUG
## (*Paracalocoris hawleyi* Knight)

During the past few years hop plants in the yards about Waterville, New York, especially in those in the vicinity of Sangerfield, have shown conspicuous injury of the foliage by perforations of the leaves, and also a stunting and deformation of the stems. In June, 1913, the vines in several yards at Sangerfield were notably injured in this manner. Careful examination of the affected plants disclosed the presence of large numbers of red nymphs with white markings. When these yards were examined early in July the nymphs were feeding on the vines and sap was flowing from the wounds made by them. A few adults were taken at that time, which later were found to belong to the family Miridae. Because of their striking color the writer has called them the hop redbug. Each year since 1913 the insect has increased greatly in numbers and has caused more and more injury. It may now be found in yards ten miles from Sangerfield, but it does not appear to have reached the Cooperstown district thirty miles distant.

Fig. 30. Work of the hop redbug on hop vine and leaves. Reduced

The writer submitted a large series of specimens for examination to H. H. Knight, who reported them as representing a new species which he described as *Paracalocoris hawleyi*. Later the determination was confirmed by W. L. McAtee, who in addition described several varieties of the species.

### NATURE OF THE INJURY

The injury caused by the hop redbug may be recognized by the deformed and stunted vines and the irregular holes in the leaves (figs. 30 and 31). The earliest injury is made evident by many light spots in the still folded leaves, and on close examination it is found that the epidermis is broken on the underside. Later, as growth of the leaf continues, a dead area is

FIG. 31. LEAVES SHOWING RESULTS OF FEEDING OF THE HOP REDBUG

produced, and when this drops out an irregular hole results. The early work is found about the middle of June, and by the middle of July the leaves may be completely riddled.

In later stages the nymphs may feed on the vines, causing a flow of sap from the punctures. As the vine grows it often becomes stunted on the side attacked, and by the continuance of its growth on the opposite side a sharp bend is formed. A plant is often weakened so that its clinging power is lost; the main stems tend to hang down, and often all the vines

of the hill slip down around the base of the pole (fig. 32). The older nymphs may feed also on the burs and the hop heads, but serious injury to these parts could not be detected by the writer. Pole yards are attacked worse than are string yards, and in string yards the vines on the poles show more injury than do those on the strings.

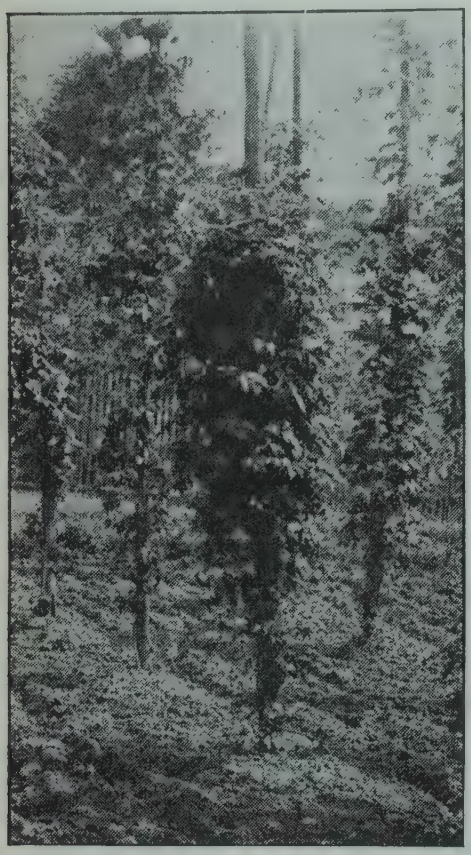

FIG. 32. A HOP HILL SO WEAKENED BY THE WORK OF THE HOP REDBUG THAT THE VINES HAVE SLIPPED DOWN THE POLE

The work of the hop redbug is similar to that described by Theobald (1895) for a related species, *Calocoris fulvomaculatus* Deg., which has caused some injury to the hop in England.

## DESCRIPTION OF THE SPECIES

### *The egg*

The egg of the hop redbug (fig. 33) is 1.6 millimeters long, 0.4 millimeter wide, and 0.2 millimeter thick. The color is dirty white. The egg is curved, with two prominent, pure white, incurving hooks on the micropyle end; one hook is pointed and the other is blunt at the tip. The surface of the egg is smooth and glossy.

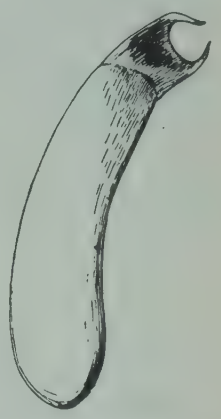

FIG. 33. EGG OF HOP REDBUG. × 24

### *The nymph*

The five nymphal stages may be described as follows:

*First stage* (fig. 34).— Length 1.3 mm. (average of ten specimens); general color light tomato red; a median variable light line extending from near the cephalic end of the head to near the posterior end of the second abdominal segment, faint in some specimens but in others distinctly white, bordered laterally on the thorax by clay-colored patches. Antennae with the basal segment slightly clubbed, tomato red, and sparsely clothed with hairs; the second segment sparsely hairy, white (2/5) and red (3/5); the third segment sparsely hairy, white ($\frac{1}{2}$) and red ($\frac{1}{2}$); the fourth segment densely hairy, clay color with a small white spot at base. Coxa of leg white, trochanter white, femur red, tibia with three red and three white bands of varying breadth, tarsus white with dark tip, claw dark. Each abdominal segment bearing a row of dark setae; head and thorax with irregularly arranged setae. Beak white with dark tip. Venter clay color. In a few cases the median line wanting, as well as all white bands,

the insect being red with the exception of the fourth antennal segment. (The description is for the most typical specimens.)

*Second stage* (fig. 35).— Length 1.9 mm.; general color slightly darker; median line broader and more distinct; clay-colored border patches indistinct; bands on antennae and legs more prominent; white spots beginning to appear around setae on abdominal segments; basal

FIG. 34. FIRST-STAGE NYMPH OF HOP REDBUG. × ABOUT 20

FIG. 35. SECOND-STAGE NYMPH OF HOP REDBUG. × NEARLY 15

antennal segment a darker red and much more hairy; terminal segments lighter except at tip. Aberrant specimens showing no median line, no white bands, faint bands on antennae and legs, or faint bands on antennae and none on legs.

*Third stage* (fig. 36).— Length 2.5 mm.; general color same as that of preceding stage; red bands on antennae and legs much darker than body; wing pads beginning to show;

FIG. 36. THIRD-STAGE NYMPH OF HOP REDBUG. × NEARLY 11

FIG. 37. FOURTH-STAGE NYMPH OF HOP REDBUG. × 9

white spots around setae more distinct. Setae longer and coarser. Some aberrant specimens as in second stage.

*Fourth stage* (fig. 37).— Length 3.1 mm.; general color as in third stage; wing pads brownish and reaching nearly to third abdominal segment; antennal segments thicker in red areas than in white; dusky spot showing around gland between third and fourth abdominal segments. Aberrant specimens as in preceding stages.

*Fifth stage* (fig. 38).— Length 4 mm.; a wide variation in color, some specimens being light red with almost transparent wing pads, others dark red with wing pads and dark spots of legs sepia; wing pads reaching almost midway between fourth and fifth abdominal segments; dusky spot around gland more prominent; in some cases two dark spots on pronotum; white spots around setae very distinct. A wide variation in markings, as in earlier stages.

FIG. 38. FIFTH-STAGE NYMPH OF HOP REDBUG. × 7

### *The adult*

The adult redbug is about 6 millimeters in length. In color it ranges from fusco-piceous to piceous, with the hemelytra sordid hyaline or pale yellowish and the cuneus reddish. The pubescence is sparse.

FIG. 39. EGGS OF HOP REDBUG INSERTED IN BARK OF CEDAR HOP POLE. × 9

## LIFE HISTORY AND HABITS

### *The egg*

The eggs of *Paracalocoris hawleyi* are inserted singly, and in groups of two, three, or four, in the bark or the wood of hop poles, to which they are attached by a secretion. In cedar bark the eggs are placed in a slit in the bark transverse to the grain, and can best be seen when the bark is torn lengthwise (fig. 39). When found in this way, the otherwise inconspicuous white cap may be located on the outside. Only one egg has been found in the hard wood of a pole, and this was in a crack just deep enough to hold it. Since nymphs are equally common in the spring on the cedar bark poles and on the wooden poles, eggs must be laid here in large numbers. The egg stage lasts from nine to nine and one-half months.

### *The nymph*

The nymphs are active, and when disturbed they crawl rapidly among the leaves and vines and into the cracks of the hop poles. At rest they

may usually be found on the undersides of the tenderest leaves, there being often from five to ten nymphs on a leaf and one hundred or more to a hill. When jarred they drop straight down to a lower leaf, to which they often adhere by everting the end of the alimentary canal. They prefer the tender leaves and vines, and therefore in August are more numerous near the tops of the poles.

The data on four specimens bred in the year 1915 are given in table 11:

TABLE 11. DATES OF TRANSFORMATION AND LENGTH OF STAGES, 1915

| Specimen | Date when egg was taken | Date of hatching | Date of beginning of nymphal stages after first | | | | Date when adult stage began | Number of days from egg to adult |
|---|---|---|---|---|---|---|---|---|
| | | | Second | Third | Fourth | Fifth | | |
| 1 | May 21 | June 13 | June 19 | June 21 | June 30 | July 8 | July 14 | 31 |
| 2 | May 21 | June 13 | June 19 | June 21 | June 30 | July 6 | July 13 | 30 |
| 3 | May 6 | June 15 | June 20 | June 24 | June 30 | July 6 | July 13 | 28 |
| 4 | May 6 | June 10 | June 15 | June 22 | June 30 | July 7 | July 12 | 32 |

Average, 30.2 days.

The specimens were bred in petri dishes in a well-ventilated, unheated field laboratory. Pieces of bark containing eggs were placed in the dishes. These were examined, and after hatching fresh food was added, each day.

FIG. 40. ADULT OF ONE VARIETY (*hawleyi*) OF HOP REDBUG. × 6½

*The adult*

The adult when disturbed drops a short distance and then flies gradually downward in a zigzag course. Adults may be found at rest on the vines, on the poles, and on the upper and under surfaces of the leaves. Technical descriptions of the species and of four varieties have been published by McAtee (1916), who examined material sent him by H. H. Knight. Of these four varieties, *Paracalocoris hawleyi* var. *hawleyi* and *P. hawleyi* var. *ancora* (figs. 40 and 41, respectively), are the common forms on the hop. The former has a pale lateral

stripe on the corium, which is not present on the latter. The latter variety is much more numerous than the former.

FIG. 41. ADULT OF ANOTHER VARIETY (*ancora*) OF HOP REDBUG. × 6½

### SEASONAL HISTORY

Overwintering eggs of *Paracalocoris hawleyi* are laid in hop poles from the middle of August until September, as determined by dissected adults. These hatch the following year from June 1 up to nearly the first of July. The nymphal period lasts for about thirty days, adults beginning to appear about the first of July. Nearly all are winged by the first of August. Adults may often be found in September but there is no evidence that these survive the winter.

### NATURAL ENEMIES

The pentatomid *Apateticus maculiventris* Say is predacious in both the nymphal and the adult form on the immature stages of the hop redbug. Eggs and nymphs of this species are common in hopyards in July and August.

One of the Nabidae, *Reduviolus subcoleoptratus* Kirby, which is present on many plants near the hopyards, has been found feeding on nymphs of the hop redbug.

A predacious red mite, *Trombidium* sp., has been observed on several nymphs.

### PREDACIOUS HABIT OF THE HOP REDBUG

Adults of *Paracalocoris hawleyi* have been found feeding on nymphs of their own kind. Nymphs have been found also feeding on the pupae of *Nematocampa limbata* Haworth (Geometridae), the larvae of *Lycia cognataria* Guenée (Geometridae), the larvae of *Hypena humuli* Harris (Noctuidae), and the pupae of *Malacosoma americana* Fab. (Lasiocampidae).

## CONTROL

In 1915 it was decided to test a tobacco extract spray as a control measure against the hop redbug. To this end nicotine sulfate, 1 pint to 100 gallons of water with 6 pounds of soap added, was applied on July 17. The material apparently killed the bugs at once. However, as 56 live nymphs were found on six sprayed hills, another spray was applied on July 19. This time Black-leaf-40, 1 pint to 100 gallons of water with 4 pounds of soap, was used. On July 20 six hills had 16 dead and 11 live nymphs present, but on July 21 no dead nymphs could be found. This is due to the fact that after the spray material dries, the nymphs drop off. The following experiment shows that whenever nymphs are reached they are killed. On July 19, when the field experiments in spraying were made, 40 sprayed specimens were placed in a laboratory cage, none of which revived. Thirty specimens sprayed with an atomizer were all killed by the same solution as was used in the field.

Since nicotine sulfate, $\frac{3}{8}$ pint to 100 gallons of water with 4 pounds of soap, will control the hop aphis (*Phorodon humuli* Schrank), the writer tried it to ascertain its effect on the hop redbug. Leaves with redbugs from vines sprayed in the field were taken into the laboratory; of 15 specimens, 6 were alive on the following day. Of 30 redbugs sprayed in the laboratory, 7 were alive twenty-four hours later. Bugs that became attached to the glass dish by means of the solution were invariably killed; those not attached often recovered. To prevent sticking, filter paper was placed in the bottom of the dish and the bugs were sprayed with an atomizer. Of 10 treated in this way, 6 were killed. It is evident that this strength is insufficient for the control of the redbug.

To be successful, spraying should be done about the third week in June, before the vines have produced large arms. Most of the nymphs will have hatched and can be reached easily at this time. Later, when the vines have become dense and many have slipped down the poles, it is impossible to reach all the bugs hidden among the mass of leaves. Poles as well as vines should be drenched, since many nymphs take refuge in the cracks and under projecting bark. Because of the agility of the bugs, it is wise to spray a hill from opposite sides at the same time when possible. Winged forms fly before they can be reached by a spray.

## THE HOP SNOUT-MOTH
## (*Hypena humuli* Harris)

The larva of the hop snout-moth was recorded in 1841 as a leaf-eating pest. It is widely distributed, occurring in most parts of the United States and southern Canada. So far as known it feeds only on the hop, and thus its distribution tends to follow that of its host (Howard, 1897). It has not been reported as a serious pest on the Pacific coast. As a rule the injury that it causes is not great, but at intervals the larvae of the second brood occur in such large numbers as to strip the hop vines of their leaves. The writer has found occasional hills in this condition but there has not been a general outbreak of the insect in the past five years.

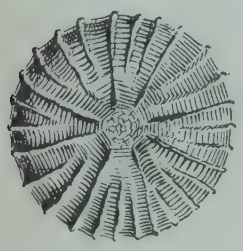

FIG. 42. EGG OF HOP SNOUT-MOTH. × 40

### DESCRIPTION

### *The egg*

The egg of *Hypena humuli* (fig. 42) is from 0.5 to 0.6 millimeter in diameter. In color it is pale yellow-white. The form is circular, slightly dome-shaped, flattened below. The surface is vertically ridged and grooved. There are apparently eight primary ribs converging at the micropyle end, with two or three secondary ribs between each pair of primaries. The micropyle is slightly flattened and irregularly reticulated.

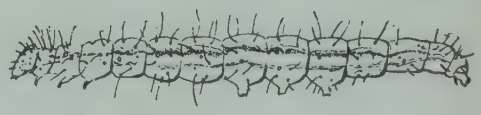

FIG. 43. FULL-GROWN LARVA OF HOP SNOUT-MOTH. SLIGHTLY ENLARGED

### *The larva*

The larva (fig. 43) is from 20 to 25 millimeters in length. The color is pale green, marked by a median longitudinal dark line and a prominent dorso-lateral white line with a fainter white line in the region of the spiracle. The head as well as the body bears prominent black tubercles. There are four pairs of prolegs including the anal prolegs.

### *The pupa*

The pupa is from 11.5 to 12.5 millimeters in length and 3.5 millimeters in greatest diameter. The body is dark brown, glossy, and faintly clothed with hairs. The cremaster consists of two large, outwardly pointing

hooks at the tip, with two smaller ones on each side. The ventral side bears a fourth pair of hooks.

*The adult*

The adult (fig. 44) is described as follows by Dr. W. T. M. Forbes:

The fore wing of the female is light wood brown, with a smoky gray trapezoidal patch resting on the inner margin rather before the middle; the base of the fore wing is more or

FIG. 44. ADULT FEMALE OF HOP SNOUT-MOTH ON A HOP LEAF. × 2

less darkened, and there is a dark shade on the outer margin, below a blackish streak which runs down obliquely from the apex; four small black tufts outline the trapezoidal patch; the usual noctuid markings are present, but are obscure, except for a row of black dots before the outer margin, representing the st. line. The hind wings and the body are similarly colored, without distinct markings. The palpi extend straight forward and are as long as the thorax, and with a tuft of hair on the face they give the appearance of a beak; the terminal joint is short and upturned. The inner margin of the fore wing is nearly straight

(unlike the clover Hypena, *Plathypena scabra*). The male is similar, but the fore wings are even dull gray, with all the markings obscure. The male is slightly larger than the female. Spread 25 to 30 mm.

## LIFE HISTORY AND HABITS

### *The egg*

The eggs of the first brood of *Hypena humuli* are deposited among the hairs on the underside of the hop leaf (fig. 45) during May, at which time

FIG. 45. EGG OF HOP SNOUT-MOTH ON LEAF. × 2½

the hops are only a few feet above ground. Eight eggs have been found on one folded leaf. These eggs, which are laid by overwintering females, may not hatch for three weeks; the exact length of the egg stage is not known. About two days before hatching, the eggs turn dark and the young larvae may be seen within. Eggs have been found in the field from May 6 to June 7.

The eggs of the second brood also are deposited on the leaves. In some cases they are laid on the older leaves near the ground, but they

may be found on tender leaves near the top of the pole. Eggs of the second brood have been found from July 28 to August 11.

*The larva*

The larva is a semi-looper, and when disturbed often throws its head in the air like a geometer. At rest it may be found stretched at full length on the underside of a leaf. Its color so protects it that it may be easily overlooked (fig. 46). When disturbed it moves its body

FIG. 46. FULL-GROWN LARVA OF HOP SNOUT-MOTH ON LEAF. NATURAL SIZE

back and forth with a wriggling motion, and drops by means of a thread. It may sometimes be found suspended in the air by this means. A newly-hatched larva (fig. 47) rarely eats thru a leaf in feeding, but when a few days older it eats out a clean-cut hole either on the margin or in the central part of the leaf. Full-grown larvae of the first brood have been taken from June 17 to July 21, and those of the second brood from August 15 to September 6.

In these experiments breeding was carried on in a field laboratory. In 1914 leaves were placed in jars of water and covered with a lamp

chimney. In 1915 larvae were kept in petri dishes to which a fresh leaf was added each day. The breeding records of 1914 and 1915 are given in tables 12 and 13.

Fig. 47. Young larva of hop snout-moth on leaf, with recently shed skin. × about 5

TABLE 12. Dates of Transformation and Length of Stages of First Brood, 1914

| Specimen | Date when egg was taken | Date of hatching | Dates of molts | Date when pupal stage began | Date when adult stage began | Number of days from egg to adult |
|---|---|---|---|---|---|---|
| 1 | May 26 | May 28 | June 1, 6, 11 | June 16 | July 1 | 34 |
| 2 | May 26 | May 28 | June 1, 5, 11 | June 23 | July 5 | 38 |
| 3 | May 26 | May 28 | June 1, 5, 12 | June 23 | July 6 | 39 |
| 4 | May 26 | May 28 | June 1, 5, 11 | June 24 | July 7 | 40 |
| 5 | May 26 | May 28 | June 2, 6, 14 | June 23 | July 6 | 39 |
| 6 | May 26 | May 28 | June 2, 6, 14 | June 25 | July 7 | 40 |

Average — Larval stage, 25.3 days; pupal stage, 13 days; egg to adult, 38.3 days.

TABLE 13. DATES OF TRANSFORMATION AND LENGTH OF STAGES OF FIRST BROOD, 1915

| Specimen | Date when egg was taken | Date of hatching | Dates of molts | Date when cocoon was spun | Date when pupal stage began | Date when adult stage began | Number of days from egg to adult |
|---|---|---|---|---|---|---|---|
| 1..... | May 6 | May 18 | ..... | June 18 | June 21 | July 8 | 51 |
| 2..... | May 6 | May 21 | ..... | June 21 | June 23 | July 8 | 48 |
| 3..... | May 28 | June 7 | ..... | ..... | July 5 | July 17 | 40 |
| 4..... | May 28 | June 8 | ..... | July 7 | July 8 | July 21 | 43 |
| 5..... | May 21 | June 13 | June 17, 26, 30 | July 7 | July 9 | July 21 | 38 |
| 6..... | June 7 | June 13 | June 17, 23, 30 | July 11 | July 12 | July 26 | 43 |

Average — Larval stage, 30 days; pupal stage, 13.8 days; egg to adult, 43.8 days.

*The pupa*

There has been much disagreement as to the manner and place of pupation of the hop snout-moth (Howard, 1897), arising from the large variety of conditions under which the process may occur. The writer has found naked pupae on the surface of the soil or just beneath the upper layer of dirt, or attached to leaves and hop poles by a few strands of silk (fig. 48). Inclosed pupae have been found fastened in cocoons in a single rolled leaf and between two leaves. They have been found also on hop poles, on dead vines, and in dirt. The cocoon may be frail or heavy. A cocoon found in the ground was covered with small particles of dirt. Pupae of the second brood are usually found naked and in the ground. Pupae of the first brood have been found between June 16 and July 26, and those of the second brood between August 19 and September 16.

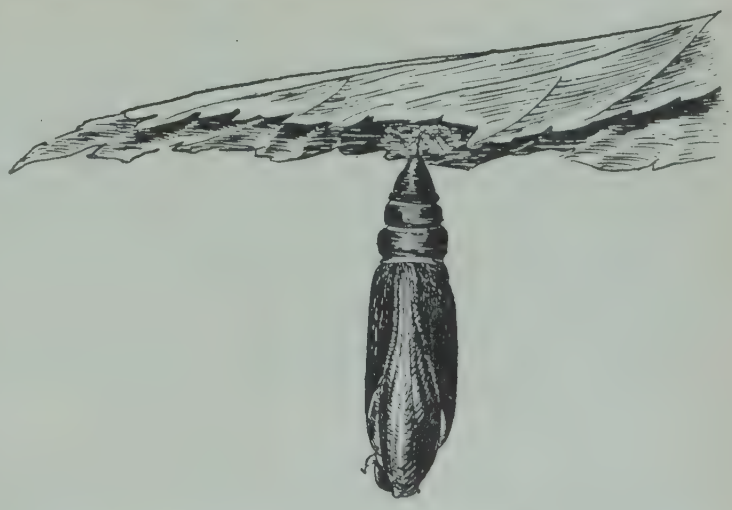

FIG. 48. PUPA SKIN OF HOP SNOUT-MOTH ATTACHED TO LEAF. × 2½

*The adult*

The adult of *Hypena humuli* has been taken in the spring and late in the fall. All pupae under observation have transformed to moths in September or October, and thus it is evident that the insect hibernates in the adult stage.

## SEASONAL HISTORY

The life history of *Hypena humuli* may vary greatly, depending on weather conditions and the date of emergence of the moths from hibernation. The following is the normal life cycle. Eggs are laid about the middle of May and hatch in about two weeks. The larvae become full-grown by July 1, the larval stage lasting about one month. The pupal stage covers about thirteen days and adults emerge about the middle of July. Eggs of the second brood are laid in from one to two weeks, and these hatch the first week of August. The larvae are full-grown at hop-picking time, early in September, when they pupate. Moths come out during the latter half of September and seek hibernating quarters.

## NATURAL ENEMIES

Nymphs of *Paracalocoris hawleyi* and adults of *Reduviolus subcoleoptratus* Kirby are both occasionally predacious on the larvae of *Hypena humuli*.

*Masicera rutila* Meign.,[5] a tachinid fly, was bred from a snout-moth larva in 1914. A larva taken into the laboratory on July 6 started to spin its cocoon on July 11 and the parasites emerged from the cocoon on August 4. In the summer of 1915, the parasite *M. eufitchiae* Towns.[5] also was bred from a snout-moth larva.

Howard (1897) reports *Exorista hypenae* also as a parasite on the larva of *Hypena humuli*.

## CONTROL

During the past three years no opportunity occurred to test control measures against the hop snout-moth. It has been reported that powdered arsenate of lead mixed with the sulfur used for the hop mildew, in a ratio of 1 to 10, has been found effective. If spraying is practiced for the hop aphis, the addition of arsenate of lead to the nicotine sulfate spray should prove a satisfactory control measure against the hop snout-moth.

[5] Determined by O. A. Johannsen.

## THE FILAMENTED LOOPER

## (*Nematocampa limbata* Haworth)

The larva of the filamented looper has been found as a leaf-eating pest of the hop in large numbers near Sangerfield, New York. It is not restricted entirely to this region, however, a few specimens having been found in some hopyards thirty miles away. The species is a general feeder, having been reported from currant, birch, stonecrop, plum, apple, crab apple, oak, and hazel, and on strawberry under the name *strawberry looper* (Packard, 1876, and Lugger, 1898). It may have come to the hop in the form of eggs on the cedar hop poles; but more probably it has migrated from other plants, as many of its known hosts occur in the region. It is widely distributed in the eastern part of this continent, being reported from Canada, New England, Minnesota, Georgia, and Illinois (French, 1878, and Lugger, 1898). While it is not of great economic importance at the present time, its numbers are increasing and it may become a serious pest.

### DESCRIPTION

### *The egg*

The egg of the filamented looper is about 0.4 millimeter in length, 0.2 millimeter wide, and 0.1 millimeter high, or of the horizontal type. The color is pale green when the egg is freshly laid, turning in from twenty-four to forty-eight hours to a dull tomato red. The egg is oblong, truncate and slightly depressed at the micropyle end and rounded at the opposite end. The surface bears faint, hexagonal reticulations.

### *The larva*

The larva passes thru four stages, which may be described as follows:

*First stage.*— Length (one day) 1 mm.; alternating tomato red and faint greenish white crossbands; head of a brown tint. One pair of prolegs and anal prolegs.

*Second stage.*— Length 4 mm. (average of five specimens); abdominal red bands more distinct; anal end suffused with red. Small tubercles appearing for the first time on second and third abdominal segments.

*Third stage.*— Length 9 mm. (average of five specimens); filaments at least equal to diameter of body in length; markings similar, but a variation occurring as in fourth stage.

*Fourth stage.*— (Detailed description of full-grown larva.) Length 18–20 mm.; color variable; general color gray, but some forms having a prominent tinge or oblique markings of shades of green, yellow, or brown. Body cylindrical. Head mottled, large, full on each

side and flattened in front. First abdominal segment bearing a sub-acute tubercle; second and third segments having a pair of long, flexible filaments of the same color as the body; those of the second segment, which are white-tipped, reaching the head when extended forward; those of the third segment about two-thirds as long as those of second segment; two small tubercles caudad of each of these appendages, and back of those of the first two abdominal segments two light yellow spots; median dark line running from the head to the first pair of filaments in dark forms; eighth abdominal segment bearing a pair of medianly joined tubercles, appearing from the side as a fleshy hump; just caudad of the hump and running to the end of the anal shield, a dark area bordered by yellow; a lateral lighter area present above and between the two pairs of prolegs.

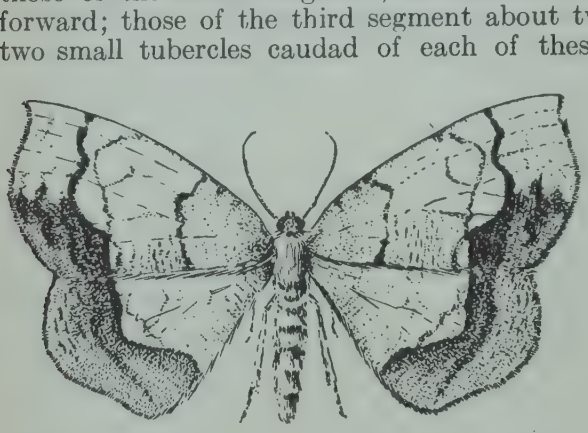

FIG. 49. ADULT MALE OF FILAMENTED LOOPER. × $2\frac{1}{3}$

### *The pupa*

The pupa is from 10 to 11 millimeters long. It is gray or pale yellow in color, and is mottled except for the membrane between the abdominal segments. The cremaster consists of two pairs of terminal outwardly curving hooks, one large and one small, and a third pair of hooks just before the apex.

FIG. 50. ADULT FEMALE OF FILAMENTED LOOPER. × 3

### *The adult*

The adult (figs. 49 and 50) is described as follows by Dr. W. T. M. Forbes :

Male straw yellow, female cream white. Fore wing with three even brown lines; t.a. line excurved, especially over cell; inner t.p. line excurved beyond cell and slightly at fold, outer t.p. incurved at points where inner is excurved and in some cases meeting it at those points; outer third of wing brown on inner half in male and everywhere but at apex in female; fringes brown. Hind wing similar, without t.a. line and with brown area more extensive; veins more or less brown, especially in female. Spread 19–25 mm.

## LIFE HISTORY AND HABITS

### *The egg*

The eggs of the filamented looper are attached by a secretion under the edge of projecting bark, or tucked in cracks of the hop poles, and

are found singly, a few in a place, or in irregular masses (figs. 51 and 52). The writer has found fifty or more eggs on a cedar hop pole by removing

FIG. 51. EGGS OF FILAMENTED LOOPER UNDER PROJECTING EDGE OF BARK OF A CEDAR HOP POLE. × 8

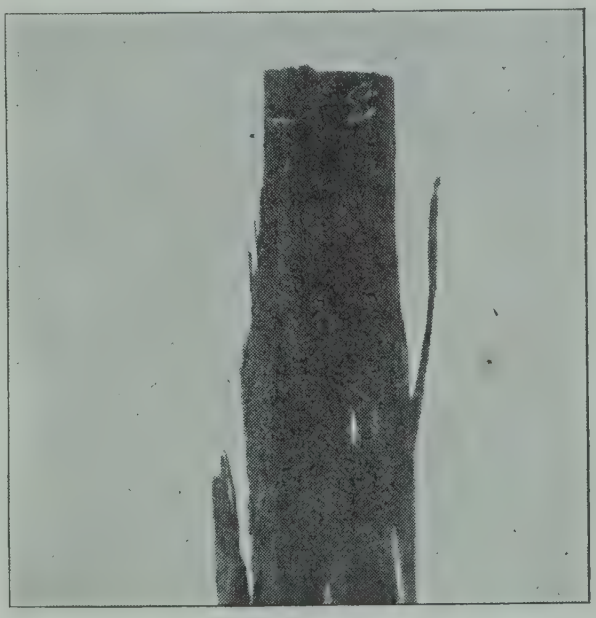

FIG. 52. EGGS OF FILAMENTED LOOPER ON A SLIVER OF A CEDAR HOP POLE. × 5

the bark and inspecting the crevices. Overwintering eggs are laid in August, and hatch from the middle of May until late in June of the following year; the egg stage is therefore about ten months. Two females under observation laid eggs as indicated in table 14:

TABLE 14. DATA ON EGG LAYING BY TWO MOTHS, 1915

| Specimen | Date when female emerged | Date when first eggs were laid | Number of eggs found on August 28 | Date preceding which moths died |
|---|---|---|---|---|
| 1 | August 15 | August 23 | 25 | September 8 |
| 2 | August 18 | August 25 | 16 | September 8 |

*The larva*

The larva moves with a looping motion (fig. 53), and when disturbed it assumes an erect attitude and projects its filaments to the limit. It

may also drop by a thread and hang in mid-air; sixty suspended larvae have been counted on one hill after the pole had been shaken. The larva feeds oftener on the margin of the leaf than in the central part. The veins of a leaf are often eaten thru in such a way that the leaf dies at that point and a dead crumpled area on the margin remains. A larva, perhaps for protection, often assumes a position resembling this dead part of the leaf. Full-grown larvae have been found from June 25 until August 18. Six specimens were bred in petri dishes in the summer of 1915, as indicated in table 15.

Fig. 53. Larva of filamented looper. × 2½

### *The pupa*

The change to the pupal stage takes place in the cracks of hop poles, in leaves curled and fastened with a few strands of silk, or when the larva is attached by silk flat against an uncurled leaf. Often the pupa is attached by a few strands of silk and hangs free from a leaf or a vine (fig. 54). In

TABLE 15. Dates of Transformation and Length of Stages, 1915

| Specimen | Date when egg was taken | Date of hatching | Dates of molts | Date when cocoon was spun | Date when pupal stage began | Date when adult stage began | Number of days from egg to adult |
|---|---|---|---|---|---|---|---|
| 1 | ..... | June 28 | July 6, 9, 13 | ..... | July 23 | August 7 | 40 |
| 2 | May 6 | June 6 | ..... | ..... | July 16 | July 29 | 53 |
| 3 | May 6 | July 16 | July 21, 25, August 1 | August 11 | August 14 | August 28 | 43 |
| 4 | May 12 | July 20 | July 24, 29, August 4 | August 11 | August 13 | August 27 | 38 |
| 5 | May 21 | July 7 | ..... | ..... | August 2 | August 15 | 39 |
| 6 | May 21 | July 5 | ..... | ..... | August 3 | August 15 | 41 |

Average—Larval stage, 28.8 days; pupal stage, 13.5 days; egg to adult, 42.3 days.

many cases small pieces of dead leaves are curled around the pupa. Pupae have been found from June 27 until August 28.

*The adult*

The brightly colored moths are common in August in the hopyards. They rest flat on the ground and on the lower leaves, with their wings half spread. The sexes are about equal in number.

FIG. 54. PUPA OF FILAMENTED LOOPER. × 4

SEASONAL HISTORY

The life history of *Nematocampa limbata* varies greatly, depending on the time of hatching of the eggs. A typical life history is as follows:

The eggs, which are laid on hop poles in the latter part of August, hatch the last of the following June. The larvae become full-grown the last of July, and enter a pupal stage which covers two weeks. Adults appear the middle of August and begin to lay eggs in about one week. There is one generation a year.

CONTROL

The control measure suggested for the hop snout-moth should hold the filamented looper in check also. On July 17, 1915, several infested hills were dusted with powdered arsenate of lead and sulfur in a ratio of 1 to 10. When the hills were examined later some live larvae were found. Since rain followed soon after the application, however, the test was not a fair one.

## THE HOP APHIS

## (*Phorodon humuli* Schrank)

The hop aphis, *Phorodon humuli* (figs. 55 and 56), is a pest wherever hops are grown. It has been known in New York State since 1863 at least (Parker, 1913), and in some years has caused an almost total loss of the crop. As the insect has been extensively studied on the Pacific coast, the writer has limited his work on the species to observations on its seasonal history and habits in New York State, and to the application of some control measures under New York conditions.

FIG. 55. WINGLESS VIVIPAROUS FEMALE OF HOP APHIS. ENLARGED

### SEASONAL HISTORY

In the eastern United States the hop aphis has been found to winter only in the egg stage on plum. Clarke (1904) reports that in California the aphides winter on hop roots. In order to obtain some evidence on this point for New York, the writer removed the dirt from three hills, placed vines covered with the insects around the hop roots, and then covered the hills. On examination the following spring, no signs of live aphides or of their eggs could be found in these hills. Additional evidence is furnished by the fact that migratory aphides have always appeared on the hop before the wingless forms.

FIG. 56. WINGED VIVIPAROUS FEMALE OF HOP APHIS. ENLARGED

Altho Riley (Riley and Alwood, 1889) reported the third generation as the one that produces winged forms in New York, it is probable that some winged forms are produced in the second generation. On May 21, 1913, full-grown lice and recent offspring were found on a plum tree near Sangerfield. On most of the leaves there was one full-grown louse, but on one leaf there were five. Some of the young of these forms had wing pads on the 4th of June. If those first found were of the first generation, the second generation produces winged forms, the same as in the Pacific hop region. Some insects of the third generation also are winged. In fact, the writer has found winged forms being produced on a plum tree under observation thru July and August, but, for unknown reasons, after the June migration there have been but few winged forms on the hop. The height of the return migration occurs during hop picking, about the first of September.

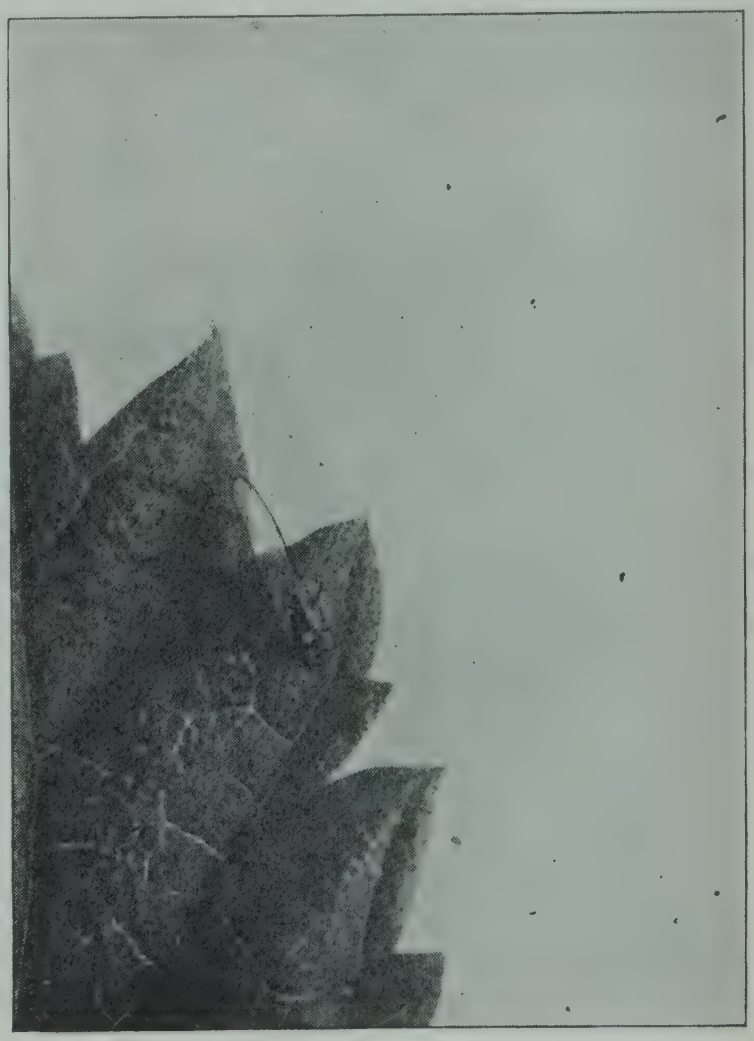

FIG. 57. WINGED VIVIPAROUS FEMALE OF HOP APHIS ON A LEAF. ENLARGED

On the hop the winged insects are found on the underside of the topmost leaves (fig. 57), there being from one to twenty or more to a leaf. The wingless descendants from these also live on the underside of the tender foliage. In August, when the lice are numerous, full-grown forms are occasionally found along the veins on the upper side of the leaves. When the young hops are formed, lice migrate to them in

large numbers. The writer has noted young lice in hop cones when the leaves were comparatively free from the insects.

Two species of ants have been found associated with the hop aphis — a large species, *Formica fusca* var. *subsericea* Say; and a small form, *Prenolepis imparis* Say.[6]

FIG. 58. ABOVE, HOPS INJURED BY THE HOP APHIS; BELOW, HEALTHY HOPS. ABOUT ONE-HALF NATURAL SIZE

### NATURE OF THE INJURY

The injury to the hop caused by *Phorodon humuli* is of two kinds: (1) the weakening of the vines and the stunting of the hop cones due to the constant removal of sap; and (2) the coating of the hops with honeydew in which a fungus, Cladosporium, grows.

The feeding of the aphides on the leaves and the vines so weakens the plant that it is common to find hills in which the vines have not climbed above the string. The vines are dwarfed and the hop cones are small, with sickly, scraggly bracts (fig. 58). This condition is found when the aphides attack the hill in numbers early in the season.

When the lice become numerous (fig. 59) the leaves glisten with the honeydew which they excrete. The entire surface of the vines and the leaves is coated with this excretion. When the lice enter the cones the bracts also are covered. The greatest damage is caused when the lice enter the full-grown hops just before picking time. They coat the hops with the honeydew, causing

[6] Both species determined by W. M. Wheeler.

the bracts to lose their crispness and making them stick together when pressed between the fingers.

The fungus Cladosporium grows in the honeydew and gives the hop a soot-covered appearance. This greatly injures the quality and makes the hops unsalable. Among hop growers it is spoken of as *black mold.* Many yards in New York were injured in this manner in 1915 and the hops were not picked, while hops from some yards that were picked are

FIG. 59. WINGLESS HOP APHIDES ON A HOP LEAF. × ABOUT 5

still unsold. The lice are much more numerous in warm, moist seasons. In 1915 the rainfall records taken showed 5.49 inches during June, 7.64 inches during July, and 9.28 inches during August. This is much above the normal for these months. A wet spring followed by a long, dry period is not so serious as continued rains near harvesting time. Under the latter condition great loss may result in a few weeks, owing to the increase of the lice, the great production of honeydew, and the growth of the black mold.

## NATURAL ENEMIES

### *Predatory enemies*

The following predatory insects have been collected feeding on the hop aphis:

| | Family |
|---|---|
| Coleoptera | |
| *Adalia bipunctata* Linn. | Coccinellidae |
| *Hippodamia convergens* Guer. (lady beetle, figs. 60 and 61) | Coccinellidae |
| *Coccinella trifasciata* Linn. | Coccinellidae |
| *Coccinella 9-notata* Herbst | Coccinellidae |
| *Coccinella sanguinea* Linn. | Coccinellidae |
| *Hippodamia parenthesis* Say | Coccinellidae |
| *Anatis 15-punctata* Oliv. | Coccinellidae |
| Neuroptera | |
| *Chrysopa oculata* Say[7] (aphis lion, fig. 62) | Chrysopidae |
| *Hemerobius stigmaterus* Fitch[7] | Hemerobiidae |
| Diptera | |
| *Syrphus americanus* Wiedemann[8] | Syrphidae |
| *Allograpta obliqua* Say[8] | Syrphidae |

FIG. 60. LARVA OF LADY BEETLE ON A HOP LEAF. × ABOUT 2

### *Parasites*

One parasite has been bred from the hop aphis —*Praon* sp.,[9] of the order Hymenoptera, family Braconidae.

## SPRAYING AND CONTROL EXPERIMENTS

The spraying operations for control of the hop aphis undertaken by growers during 1915 were observed by the writer. These are here described, and some original data on spraying and dusting are given.

[7] Determined by R. C. Smith.
[8] Determined by O. A. Johannsen.
[9] Determined by A. B. Gahan, thru the kindness of Dr. L. O. Howard.

The first spraying of the season was done on the Louie farm, at Schuyler Lake. The material used was nicotine sulfate (Black-leaf-40) in a solution of 1 gallon to 2000 gallons of water, with whale-oil soap added, 4 pounds to 100 gallons. A Friend pony outfit (fig. 63), with three leads of hose, was used. Two men, with 6-foot poles, 30°-angle nozzles, and 15 feet of hose, covered two rows each, and the third man, going behind, covered the high arms and the tops of the poles. Calyx nozzles of the Vermorel type, throwing more than the usual quantity of material, were used. The tank had a capacity of 150 gallons, and with a $1\frac{1}{2}$-horse-power engine a pressure of over 150 pounds was maintained. The cost for spraying two acres a day was as follows: four men, $8; one horse, $1; 800 gallons of spray material, $6; total, $15 for two acres, or $7.50 an acre. Hops of a fine quality were produced.

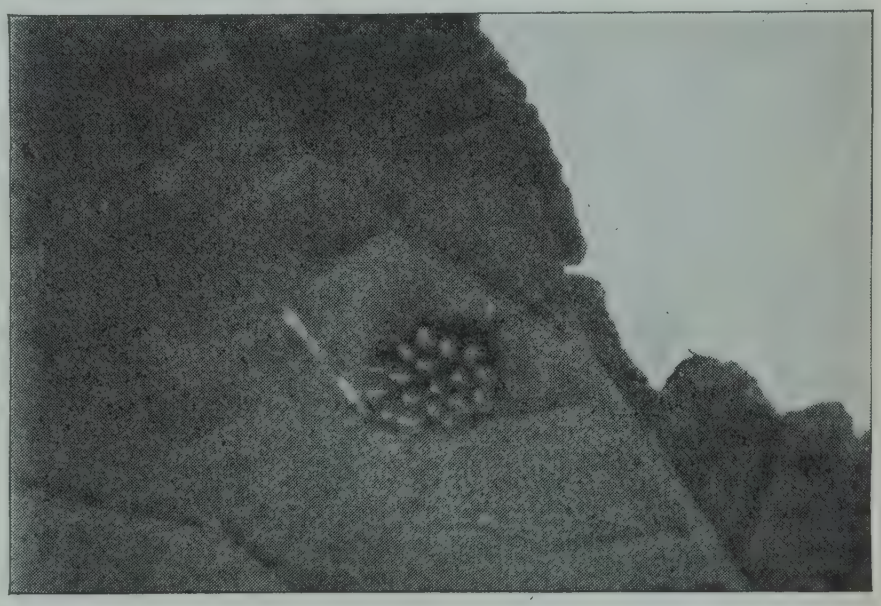

FIG. 61. EGGS OF LADY BEETLE ON A HOP LEAF. ENLARGED

FIG. 62. APHIS LION, THE LARVA OF WHICH IS PREDACIOUS ON THE HOP APHIS. ENLARGED
(Photograph by H. H. Knight)

Under the direction of F. M. Blodgett, about ten hopyards were sprayed. In one yard, near Waterville, a pressure of 165 pounds was maintained and 600 or more gallons of spray material were used to the acre. In all cases nicotine sulfate (1–2000) and whale-oil soap (4–100) were used. During these operations the writer picked sprayed leaves and made counts

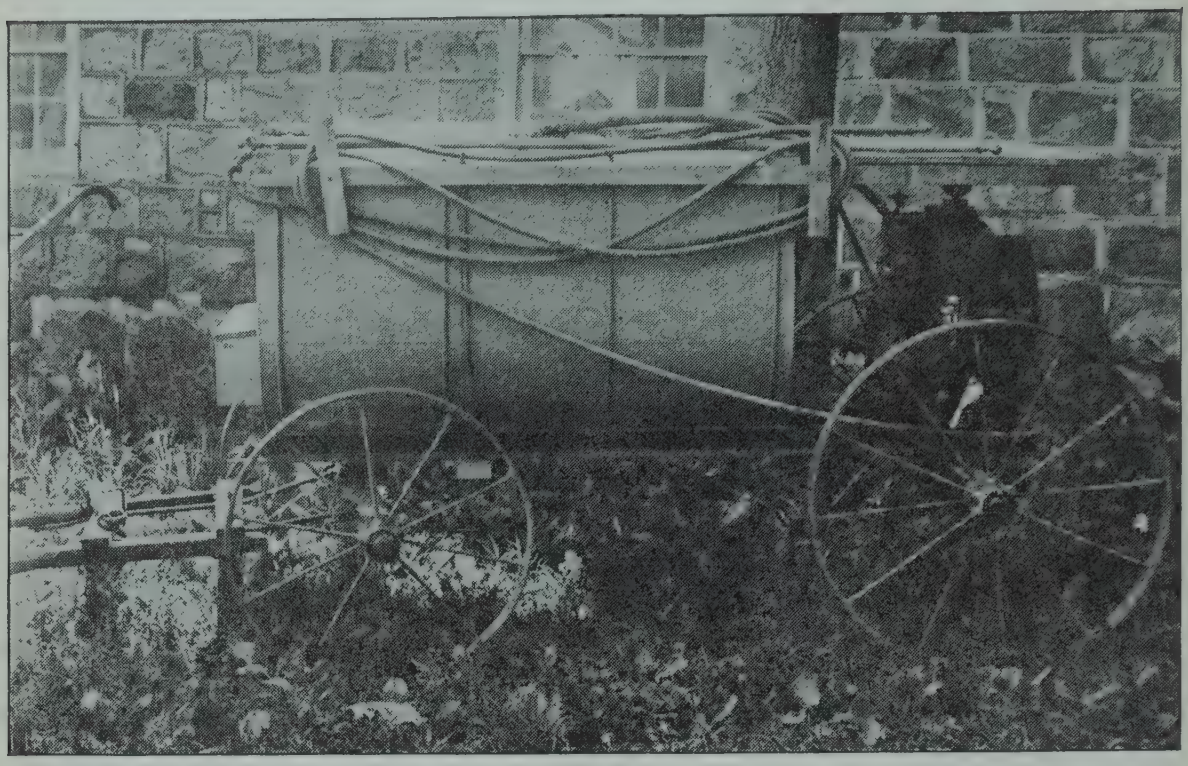

FIG. 63. SPRAYER USED ON THE LOUIE FARM — A COMMON TYPE

to test the effectiveness of the spray. The results of these counts are given in table 16:

TABLE 16. RESULTS OF SPRAYING EXPERIMENTS WITH BLACK-LEAF-40, 1915

| Yard | Date of spraying | Date of count | Number of lice found | Number dead | Per cent of control | Number of leaves used | Remarks |
|---|---|---|---|---|---|---|---|
| Hatch ..... | July 27 | July 28 | 830 | 821 | 98.9 | 20 | All lice counted |
| Hatch ..... | August 18 | August 19 | 103 | 100 | 94.3 | 12 | Only full-grown lice counted |
| Hatch ..... | August 19 | August 20 | 356 | 352 | 98.9 | 12 | Only full-grown lice counted |
| Hewett ..... | August 31 | September 2 | 721 | 698 | 96.8 | 20 | All lice counted |

Sulfur is used by growers to control the hop mildew, and so the writer tried combinations of sulfur with nicotine sulfate, using different stickers, to see its effect on the lice, paying no attention to the control of the hop mildew. The results are given in table 17:

TABLE 17. RESULTS OF EXPERIMENTS TO TEST BLACK-LEAF-40 WITH SULFUR IN VARIOUS FORMS, 1915

(Only full-grown lice were counted. B.L.40 = Black-leaf-40, 1-2000; L.S. = lime-sulfur, 1-40; Sp. = soap, 4-100; S = sulfur)

| Material used | Date of spraying | Date of first count | Number of leaves used | Number of lice found | Number alive | Per cent of control | Date of second count | Number of leaves used | Number of lice alive |
|---|---|---|---|---|---|---|---|---|---|
| B. L. 40, Sp., S | July 16 | July 17 | 12 | 828 | 11 | 98.7 | July 24 | 12 | 4 |
| B. L. 40, L. S. | July 16 | July 17 | 12 | 360 | 16 | 95.5 | July 24 | 12 | 30 |
| B. L. 40, L. S., Sp. | July 16 | July 17 | 12 | 574 | 3 | 99.5 | July 24 | 12 | 4 |
| B. L. 40, Sp. | July 17 | July 20 | 12 | 77 | 2 | 97.4 | July 24 | 12 | 1 |

Lime-sulfur leaves a smeary coating and should not be used just before the hops are to be picked. None of the sprays tested injured the hops.

There has been much demand among growers for a louse-killing material that can be applied in a dust form with the sulfur used for the hop mildew. With this in view an experiment was carried on in two parts. In one (W, table 18) the hills were sprayed with water and the material was dusted on; in the other (D) the material was applied to the dry leaves. Both the upper and the under sides of the leaves were well covered in each case. The results of these experiments are given in table 18:

TABLE 18. RESULTS OF DUSTING EXPERIMENTS, 1915

(Ten leaves of each kind were examined, and only adult lice were counted)

| Material used | Date of application | Date of count | Number of lice found | Number dead | Number alive | Per cent of control |
|---|---|---|---|---|---|---|
| Tobacco dust.....(W) | August 6 | August 10 | 249 | 12 | 237 | 4.8 |
| (D) | August 6 | August 10 | 125 | 4 | 121 | 3.2 |
| Tobacco dust and sulfur, 1-1.....(W) | August 6 | August 10 | 243 | 6 | 237 | 2.5 |
| (D) | August 6 | August 10 | 86 | 0 | 86 | 0.0 |
| Tobacco dust and flour, 1-1.....(W) | August 6 | August 10 | 138 | 57 | 81 | 41.3 |
| (D) | August 6 | August 10 | 116 | 5 | 111 | 4.3 |
| Tobacco dust and soap, 3-1.....(W) | August 6 | August 10 | 128 | 80 | 48 | 62.5 |
| (D) | August 6 | August 10 | 78 | 7 | 71 | 9.0 |
| Tobacco dust, sulfur, and soap, 2-3-1(W) | August 6 | August 10 | 126 | 113 | 13 | 89.7 |
| (D) | August 6 | August 10 | 49 | 3 | 46 | 6.1 |

It is evident that dusting was not effective. The tobacco dust, which was used as the killing agent, was useless even when the leaves were wet. A few aphides were stuck to the leaves by the flour when wet. The powdered soap, when wet, was efficient, but inasmuch as this soap costs 22 cents a pound it cannot be considered practicable. Only a driving rain of long duration could wet the underside of the leaves, and with such a rain there would be a tendency for the lice to be washed off and a spray applied would be of little use.

If the lice on the plum are killed, the infestation will be cut down. This cannot be considered as a sure control, because scrubby plum trees along fence rows are prolific breeding centers. The writer found many winged lice in one corner of a hopyard. In searching for the source he found a small plum tree, less than three feet high and almost concealed by grass, completely covered with the pests.

Lice are apparently carried long distances by the wind. Winged forms have been found in large numbers in yards where the owner declared there were no plum trees within half a mile. A thoro search by the writer did not disclose the source of the infestation. It is possible that some other host may exist, but none has been found, even tho many kinds of trees and bushes have been examined for lice of this species.

### *Recommendation*

The following practice is recommended for control of the hop aphis: Spray the last week of June or the first week of July with nicotine sulfate (1–2000, or $\frac{3}{8}$ pint to 100 gallons) and soap (4–100). Use a one-horse sprayer with a 150-gallon tank and three leads of hose. Use two 6-foot poles with 30°-angle nozzles and 15 feet of hose, and one longer pole without the angle and with 30 feet of hose. Let each of the men with the short poles cover the lower vines and arms of two rows, and let the man behind, with the long pole, cover thoroly the higher vines and arms (fig. 64). A Vermorel-type nozzle throwing a coarse spray is efficient, but a nozzle producing a mist spray is recommended on the Pacific coast. The soap should be melted in quantity; a large iron kettle is convenient for this purpose. If the yard is distant from the water supply, a filling wagon is necessary.

It is important to hit all lice. Those on the higher, tenderer leaves, where the winged forms collect and where the migration to the hop cones takes place, must be killed. Late spraying is ineffective, as some lice cannot be reached because of the growth of the arms and because some will have migrated into the burs and the hops. If all winged lice are killed early in the season, there will be none to reproduce later.

FIG. 64. SPRAYING HOPS WITH A POWER SPRAYER
(Photograph by C. R. Crosby)

Because of this pest, New York State in the past has lost hops which have cost thousands of dollars to raise. Spraying should be considered as crop insurance. While it will not result in saving a crop every year, it will improve the quality of the product and raise the price when the average quality is low. The history of the past few years proves that hop dealers want hops of a good quality, and that such hops usually sell readily and at an advantageous price.

## THE RED SPIDER, OR SPIDER MITE

(*Tetranychus telarius* Linnaeus)

The red spider occasionally appears in the hopyards of New York, but has never caused any serious damage here such as it has on the Pacific coast. With the shorter growing season and the cold winters, it is not likely that it will become a serious pest.

The mites were observed on weeds and hop poles on May 6, 1915, and it is probable that they hibernate mainly as adults in cracks of the poles or on dead weeds around the yards. The presence of the mite may be detected by small, light yellow spots at the base of a leaf between the main veins. If the underside of such a leaf is examined, silken webs will be found and beneath these the mites usually rest. Later the leaves turn yellow and a few drop off. The lower leaves are first attacked, and as these leaves are killed the mites move upward and some enter the hops. A few mites were found in the hops of one yard in the dry summer of 1913.

### CONTROL

It has never been necessary to adopt control measures against the red spider in New York hopyards. In 1913 a few hills were sprayed with flour paste (8–100), and others with lime-sulfur (1–80) and flour paste (4–100), as recommended by Parker (1913, a and b) in consequence of his work on the Pacific coast. The action of both materials was satisfactory, but, as neither spray kills the eggs and since only one application was made, mites were present a few weeks later. Not all the mites were killed, as the mist spray which was used did not always penetrate the webs to the mites beneath. If desirable, flour paste or lime-sulfur may be applied in combination with the Black-leaf-40 used for control of the hop aphis. Black-leaf-40 with soot will kill many of the mites, and if used at a high pressure it might give control.

## THE HOP MERCHANTS

(*Polygonia interrogationis* Fabricius and *P. comma* Harris)

The chrysalides of the two well-known butterflies *Polygonia interrogationis* and *P. comma* are called *hop merchants*, and are familiar to growers

because of a superstition that is connected with them. If the spots on the chrysalis (fig. 65) are golden, it is supposed that the hops will be of good quality and will bring a high price; but if the spots have a silver tint, the opposite is to be expected. Growers do not as a rule connect the spiny larva (figs. 66 and 67) or the brightly colored butterfly (fig. 68) of the two species with the hop merchant, and yet these insects have been of such popular interest to the student of nature that their life histories, food plants, and dimorphism have been understood for many years. There are usually two broods a year, and the chrysalides of the second brood, often found at hop-picking time, are of great interest to hop pickers. The insects are not of economic importance, for aside from a few leaves eaten by the larvae they do no harm.

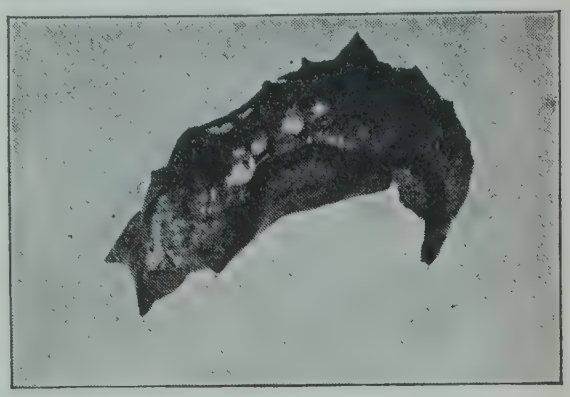

FIG. 65. CHRYSALIS OF HOP MERCHANT. ABOUT NATURAL SIZE
*Polygonia interrogationis*

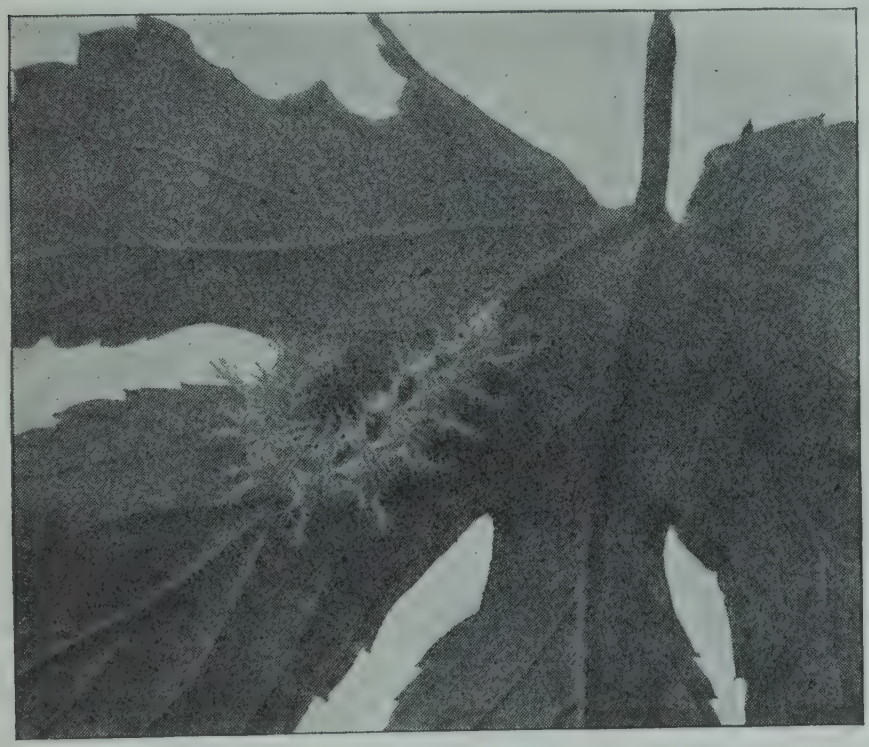

FIG. 66. LARVA OF HOP MERCHANT. ABOUT NATURAL SIZE
*Polygonia interrogationis*

Many of the larvae of both species are parasitized by a bright green chalcis fly (*Pteromalus vanessae* Harris).[10] The writer placed caterpillars of *Polygonia interrogationis* in a cage in July, and when examined on August 24 many of the chrysalides had taken on a distinctly yellow color and

[10] Determined by A. B. Gahan, thru the kindness of Dr. L. O. Howard.

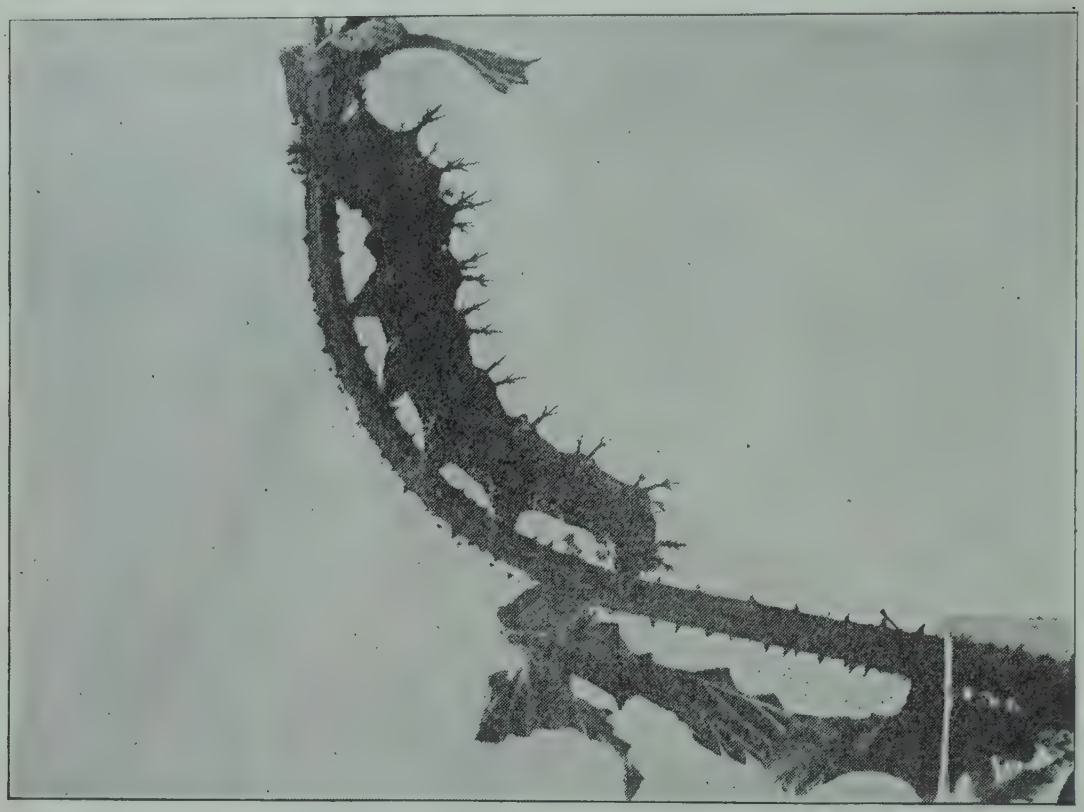

FIG. 67. LARVA OF HOP MERCHANT. NATURAL SIZE
*Polygonia interrogationis*

FIG. 68. ADULT OF HOP MERCHANT. SLIGHTLY REDUCED
*Polygonia comma*
(Photograph by H. H. Knight)

parasites were found to be emerging thru holes in their sides. One chrysalis contained 12 full-grown chalcides. Howard (1897) believes the insects are held in check by this means.

## LEAF HOPPERS

(*Empoasca flavescens* Fabricius and *E. flavescens birdii* Goding)

Leaf hoppers (*Empoasca flavescens* Fab. and the variety *E. flavescens birdii* Goding) are often present in large numbers on the hop plant. Twenty or more may be found on the underside of one of the lower leaves, but the insects are never found on the burs or the hops. The insect probably winters as an adult in New York, since specimens have been found near yards and on hop poles during the first part of May of each year. In Illinois adults taken on December 16 emerged from hibernation on April 20 (Forbes, 1900). In 1915 nymphs of the first brood began to appear on the hop the middle of June; these transformed to adults about the middle of July, and from this time forward all stages could be found on the leaves. A second brood occurs every season, and in dry seasons there is probably a partial third brood. The insects seem to be more numerous in dry seasons. In 1913, when the hop aphis was scarce, there was a general outbreak of leaf hoppers.

When leaf hoppers are numerous the leaves lack vitality and turn yellow. In June, 1915, in one badly infested yard the leaves were much curled. At that time the writer attributed the injury to leaf hoppers, but as this yard was frostbitten early in the season it is possible that this conclusion was incorrect. Accordingly an experiment was undertaken to test the point. Several hundred leaf hoppers were placed in paraffined bags which were tied on the arms of a hop vine in a yard nearly free from the insects. On July 14, over a month later, when the bags were examined, the leaf hoppers were all dead and the leaves in one bag showed curling. In the other bags there was no curling and the leaves appeared much as in the check bags.

*Empoasca flavescens* is a general feeder. The writer has collected specimens on plum in the fall, and the variety *birdii* has been previously reported on beans, weeds, walnuts, and apple trees (Forbes, 1900); in Illinois it often causes damage to the last-named host. *E. flavescens birdii* has a smoky band across the hemelytra, which is wanting in *E. flavescens*.

The writer has taken both forms in the same hopyard. According to Forbes (1900) the species is widespread; it has been reported from New York to the District of Columbia, and from California and Mexico.

### CONTROL

While spraying for the red spider it was observed that flour paste often sticks the nymphs of leaf hoppers to the leaves. The usual aphis spray of nicotine sulfate and soap destroys them readily.

## THE MILLIPEDE
## (*Julus caeruleocinctus* Wood)

A species of millipede (*Julus caeruleocinctus*,[11] fig. 69) seems to be always present in large numbers in hopyards. Several hundred specimens, in all stages of development, may often be taken from a single hill. They are the most plentiful where there is decaying matter, and are especially numerous in dead and dying hop roots.

FIG. 69. A MILLIPEDE FOUND IN HOPYARDS. × 2½

No damage is caused by the millipede after the hop vines have become hardened. In order to test this, a cage was sunk around a hop hill and several hundred millipedes were placed in it. No damage to the vines resulted. In May, when the succulent hops are just coming up, shallow areas are occasionally eaten in the stems. These soon grow over without seriously retarding the growth of the vines.

It was observed in the experiments for control of the hop grub, that carbon disulfid applied in large quantities often proved fatal to millipedes.

## THE LEAF MINER
## (*Agromyza* sp.)

The larva of a dipterous leaf miner (*Agromyza* sp.) is often found working in the lower leaves of the hop during May and June. On June

[11] Determined by R. V. Chamberlin.

7, 1915, the serpentine mines caused by the insects (fig. 70) were very numerous at Waterville. Specimens of the leaf miner were bred and

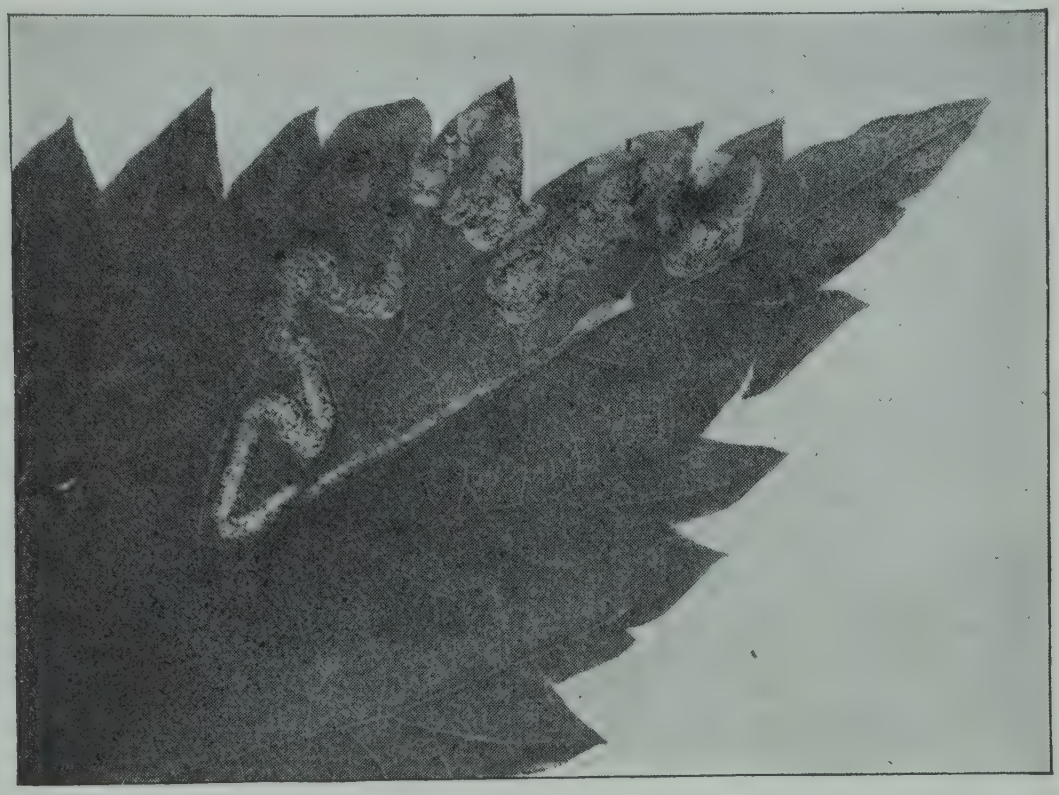

FIG. 70. MINE OF A DIPTEROUS LARVA IN A HOP LEAF. SLIGHTLY ENLARGED

identified for the writer by S. W. Frost. The insect belongs to the Agromyzidae and is thought to be a new species.

### FLEA BEETLES

(*Psylliodes punctulata* Melsh., and others)

Flea beetles are occasionally found on the hop in New York, but they have never been numerous enough to cause serious damage. The writer has found from five to ten on a hill, and a lower leaf here and there will show the work of the insects in the form of small holes between the veins. In the hop sections of the Pacific coast, the hop flea beetle (*Psylliodes punctulata*) has caused great damage and has been a difficult pest to control (Parker, 1909). The following species have been taken by the writer on the hop plant: *Psylliodes punctulata* Melsh., the punctured flea beetle (the hop flea beetle of the Pacific coast); *Epitrix cucumeris*

Harr., the potato flea beetle; *Psylliodes convexior* Lec.; *Systena frontalis* Fab., the red-headed flea beetle.

## LEAF ROLLERS

(*Archips rosaceana* Harris and *A. argyrospila* Walker)

The oblique-banded leaf roller (*Archips rosaceana*) is occasionally found on the hop. The white egg masses are found on the upper side of the leaf, and are easily mistaken for a healthy spot of the hop mildew. An egg mass taken to the laboratory on July 15, 1915, hatched on July 18. Two of the larvae were separated and supplied with food. One pupated on August 15 and emerged on September 5; the other pupated on August 17 and emerged on September 6. From other larvae taken to the laboratory, two parasites (*Meteorus* sp. and *Itoplectis conquisitor* Say [12]) were reared. The newly hatched larvae destroy a few leaves but do little real damage.

A larva of the fruit-tree leaf roller (*Archips argyrospila*) was found on the hop on May 6, 1915. At that time it was feeding on the tender tissues of the tip, and had produced a muffle head similar to that caused by the larva of *Gortyna immanis*.

## MISCELLANEOUS INSECTS ON HOP

In the following list are given a number of additional species of insects that are found on hops, together with data regarding them:

| Species | Stages | Parts of plant infested | Time of appearance | Numbers | Injury caused |
|---|---|---|---|---|---|
| *Lygus pratensis* Linn | Nymph, adult. | Lower leaves. | July–August | Numerous. | None |
| *Lygus invitus* Say | Nymph, adult. | Lower leaves. | July–August | Numerous. | None |
| *Phytocoris* sp | Adult | Lower leaves. | | Few | None |
| *Diabrotica 12-punctata* Fab. | Adult | Lower leaves. | | Few | None |
| *Corymbites cylindriformis* Herbst | Adult | Hop heads, leaves | May | Few | Slight |
| *Lachnosterna* sp | Larva | Roots | All seasons | Few | None |
| *Telephorus tuberculatus* Lec. | Adult | Leaves | August–September. | Few | None |
| *Telephorus bilineatus* Say | Adult | Leaves | August–September. | Few | None |
| *Podabrus rugosulus* Lec. | Adult | Leaves | August–September. | Few | None |
| *Mamestra picta* Harr | Larva | Leaves | June | Few | None |
| *Peridroma margaritosa* Haw | Larva | Leaves | June | Few | None |
| *Erannis tiliaria* Harr | Larva | Leaves | May–June | Few | None |
| *Lycia cognataria* Guen | Larva | Leaves | June | Few | None |
| *Automeris io* Fab | Larva | Leaves | August–September. | Few | None |
| *Tropaea luna* Linn | Larva | Leaves | August–September. | Few | None |
| *Notolophus antiqua* Linn. | Larva | Leaves | August–September. | Few | None |
| *Hemerocampa leucostigma* Smith & Abbott | Larva | Leaves | August–September. | Few | None |

[12] Determined by A. B. Gahan, thru the kindness of Dr. L. O. Howard.

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*humuli*.] Larva on hatching enters head of hop and causes head to hang down, forming a muffle head. When larva is one-half inch long it leaves head and enters vine, which becomes hard and hollow as flow of sap stops. About June 21 larva leaves head and feeds on outside of vine, nearly or entirely severing it. Pupation occurs about the middle of July in a rude cell; the pupae hibernate as a rule, but a few adults emerge in the fall. Control: Cultivate skunks; destroy pupae in spring; pinch heads of hops; expose roots about one week in June and add a mixture of coal and wood ashes or ammoniated phosphate, then hill high, and vines stimulated by fertilizer will send out rootlets to get food. *Calosoma calidum* is predacious on young grubs. *Hydroecia obliqua* considered a Western variation of *H. immanis*.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# A FIFTH PAIR OF FACTORS, *Aa*, FOR ALEURONE COLOR IN MAIZE, AND ITS RELATION TO THE *Cc* AND *Rr* PAIRS

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# A FIFTH PAIR OF FACTORS, *A a*, FOR ALEURONE COLOR IN MAIZE, AND ITS RELATION TO THE *C c* AND *R r* PAIRS

# A FIFTH PAIR OF FACTORS, *Aa*, FOR ALEURONE COLOR IN MAIZE, AND ITS RELATION TO THE *Cc* AND *Rr* PAIRS[1]

R. A. Emerson

Students of the genetics of maize are familiar with four pairs of aleurone-color factors, namely, *Cc*, *Rr*, *Pr pr*,[2] and *Ii*. To East and Hayes (1911) and to East (1912) belongs the credit for establishing the existence of these factors and for determining their interrelations. The writer also has been able to present data bearing on the inheritance of aleurone color (Emerson, 1911, 1912, 1915). The purpose of this paper is to report the discovery of a fifth pair of aleurone-color factors,[3] to give the data necessary in establishing its existence, and to note certain other factors, genetic and otherwise, concerned in aleurone-color development.

The present status of information with respect to the four factor pairs listed above may be stated briefly as follows: Two dominant factors, *C* and *R*, must be present in order that any aleurone color may develop. When *Pr* also is present the color becomes purple, while in the homozygous presence of its recessive allelomorph, *pr*, the color is red. The presence of *I*, alone or in combination with the other factors, insures colorless or nearly colorless aleurone. It is perhaps unnecessary, in following East and Hayes in the use of the symbol *I*, to accept the idea that it is an inhibitor of aleurone color. It can be held instead that colored aleurone is produced thru the interaction of *i i* with *C* and *R*.

The factors *Pr* and *I* in the writer's cultures are doubtless the identical factors studied by East and Hayes. It is a simple matter to determine their presence or that of their recessive allelomorphs by means of appropriate aleurone-color testers. Crossing with homozygous red is obviously the test for *Pr* and *pr*, and with homozygous red or purple the test for *I* or *i*. These factors are of little concern in the account here given.

---

[1] Paper no. 69, Department of Plant Breeding, Cornell University, Ithaca, New York.

[2] While the writer and his coworkers realize the importance of following prior usage with respect to genetic symbols, *P* is now used by them to designate a series of multiple allelomorphs affecting pericarp color, superscripts being employed to distinguish the several members of the series. For this purpose it seems essential to use a single letter. The purpling factor pair for aleurone color, therefore, is now given the designation *Pr pr*.

[3] This factor pair was first announced by the writer in an unpublished paper presented before the New York meeting of the Botanical Society of America in December, 1916. It has been referred to in papers by Lindstrom (1917, 1918) and Bregger (1918).

While there is reason for the belief that the factor pairs known to th writer as *C c* and *R r* are the ones studied by East and Hayes, there no assurance that the writer's *C* may not be their *R* and the writer *R* their *C*. Since there was no way of determining which of these, either, is the fundamental color factor and which is the reddening facto the symbols were assigned arbitrarily to certain stocks. The presence *C* or of *R* in other lots can now be determined by appropriate use these original stocks, as becomes evident later. An exchange of materi with Messrs. Collins and Kempton has made it possible to determin that their *C* and *R* are the same as the writer's. The writer is indebte to Mr. E. G. Anderson for making these determinations, and for oth assistance in the studies of aleurone color.

The peculiar interrelations of *C* and *R* make possible, as is well know not merely the monohybrid ratio of three colored to one colorless, bu also the dihybrid, 9:7, ratio. The former is of course given by eithe *C c R R* or *C C R r*, while the latter results only from *C c R r*. It follow naturally that from the latter there appear three classes of whites, namely *C r*, *c R*, and *c r*. The first two of these, when intercrossed, giv a colored $F_1$ and an $F_2$ of 9 colored to 7 colorless. All this is so we known — for maize no less than for sweet peas, stocks, and other forms — that a 9:7 $F_2$ ratio is now commonly expected when a colored $F_1$ is pro duced by a cross of colorless parents.

## EXPERIMENTAL RESULTS, $F_2$ GENERATION

The records published by East and Hayes (1911) and by East (1912) and certain of the writer's records, exhibit $F_2$ ratios closely approximating 9:7. From other crosses made by the writer between whites not closely related in the main to those previously studied, colored $F_1$'s were obtained but in $F_2$ the results were too far from a 9:7 ratio to be treated as such The records of these $F_2$ progenies, sixty-one in all,[4] are given in table (page 266). Most of them came from crosses of colorless with colorless but a few were from crosses of colored with colorless parents. The $F_1$'s were colored in all cases. The percentages of colorless seeds in the $F_2$ lots ranged from 44.9 to 66.5, with an average of 57.79, whereas the theoretical percentage of colorless in true 9:7 $F_2$ progenies is 43.75

[4] Records of twenty-six of these progenies were furnished the writer by Mr. E. W. Lindstrom, who obtained them in connection with studies of linkage between certain aleurone and chlorophyll factors.

thus even the lower extreme is above the average expected on the basis of a 9:7 ratio. Frequency distributions of these sixty-one percentages of $F_2$ whites are shown in figure 71, B.

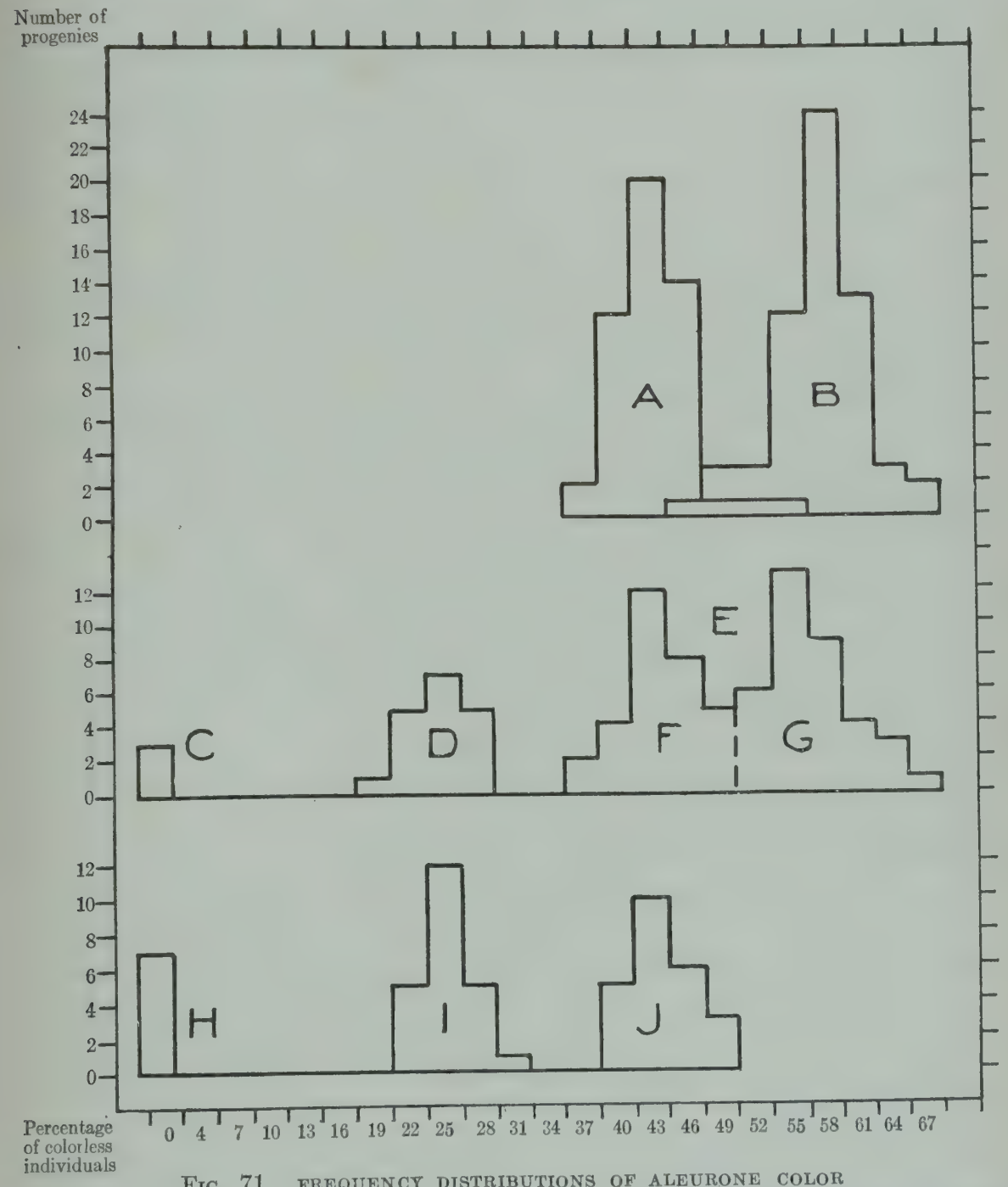


FIG. 71. FREQUENCY DISTRIBUTIONS OF ALEURONE COLOR

Percentages of colorless individuals in the progenies of plants heterozygous for aleurone color. A and B, $F_2$ progenies; C to G, $F_3$ progenies from B; H to J, $F_3$ and $F_4$ progenies from A

The total number of individuals of the sixty-one $F_2$ progenies was 25,289. The observed numbers of colored and colorless individuals are compared with the theoretical expectancy from a 9:7 ratio in the following statement:

| | Colored | Colorless | Total |
|---|---|---|---|
| Observed | 10,674 | 14,615 | 25,289 |
| Calculated | 14,225 | 11,064 | 25,289 |
| Difference | —3,551 | +3,551 | 0 |

The probable error, based on the expected ratio of 9:7 and the observed number of individuals, is ±53.38. The odds against the possibility of the occurrence of a deviation of 3551 thru errors of random sampling are therefore inconceivably great.

While it is perhaps unnecessary to call attention in any other way to the divergence between observation and expectation, it is of interest to note that the observed ratio per sixteen is 6.753:9.247, or practically a 7:9 instead of a 9:7 relation.

For comparison, records of fifty-one $F_2$ progenies, from stocks not closely related in the main to the foregoing, are brought together in table 2 (page 268). The percentages of colorless seeds ranged from 36.0 to 53.7. The average percentage for the lot as a whole was 42.91±0.28, while 43.75 is the theoretical percentage for a 9:7 ratio. The deviation of 0.84 from the expected percentage is therefore three times the probable error of the observation. The odds against the occurrence of a deviation so great as this being due to random sampling, are 22.3 to 1. Of the deviations for the separate progenies (table 2), however, only two are greater, relative to their probable errors, than the deviation for the lot as a whole. These two are 3.2 and 3.8 times the probable errors, the corresponding odds being approximately 31 to 1 and 95 to 1, respectively, against such deviations being due to chance. Six other progenies have deviations from two to three times the corresponding probable errors, while nineteen have deviations from 1 to 1.9 times the probable errors and twenty-four have deviations less than the probable errors. While, therefore, most of these deviations are probably not significant, it happens that, of the fifty-one progenies, thirty have minus and only twenty have plus deviations, the remaining deviation being zero. While this departure

from equality in the number of plus and minus deviations is less than twice the probable error, it is nevertheless sufficient to give a rather large minus deviation for the fifty-one progenies as a whole.

The total number of individuals in these fifty-one $F_2$ progenies was 14,714. The numbers of colored and colorless individuals observed are compared with the expected numbers in the following statement, the probable error being 41.2:

| | Colored | Colorless | Total |
|---|---|---|---|
| Observed | 8,402 | 6,312 | 14,714 |
| Calculated | 8,277 | 6,437 | 14,714 |
| Difference | +125 | —125 | 0 |

Expressed as a ratio with a total of sixteen, the relation of colored to colorless individuals in the fifty-one progenies as a whole is 9.136:6.864, thus approximating the expected 9:7.

The distribution of percentages of colorless seeds of the fifty-one $F_2$ progenies is shown in figure 71, A. A glance at the two frequency distributions (fig. 71, A and B) reveals the striking dissimilarity between them. The fact that there is some overlapping of the two distributions does not materially lessen their distinctiveness. The one indicates definitely a dihybrid, 9:7, ratio, while the other suggests a trihybrid, 27:37, ratio, as explained below.

### THE THREE-FACTOR HYPOTHESIS

If, in addition to the four factor pairs listed earlier in this account, there be assumed a fifth pair, *A a*, of such a nature that aleurone color develops only in the presence of all the three dominant factors *A*, *C*, and *R*, a 27:37 $F_2$ ratio should result whenever $F_1$ is heterozygous for the three factors. From an $F_1$ of the formula *A a C c R r*, eight combinations of the factors should appear in $F_2$ in the numerical relation of 27:9:9:9:3:3:3:1. The 27 having all the dominant factors will be colored, and the other 37, since they all have at least one homozygous recessive pair, will be colorless.

The theoretical percentage of colorless seeds in a 27:37 ratio is 57.81. The observed percentages for the sixty-one progenies recorded in table 1,

it will be recalled, ranged from 44.9±4.0 to 66.5±1.6. The average percentage of colorless for the lot as a whole was 57.79±0.21, thus corresponding almost exactly with the percentage expected from a 27:37 ratio, the deviation being much less than the probable error. While most of the deviations from the theoretical percentage among the sixty-one progenies are probably due to chance, a few are perhaps significant. The deviations divided by the corresponding probable errors are from 0 to 0.9 in twenty-four cases, from 1 to 1.9 in sixteen cases, from 2 to 2.9 in fourteen cases, from 3 to 3.9 in six cases, and 5.4 in one case. In the last case particularly there is only one chance in several thousand that so great a deviation could be due to the errors of random sampling.

While some of these deviations cannot be regarded as due to mere chance, and while the one percentage of 66.5 fits well the theoretical percentage of 68.4 expected in case four factors are concerned — deviation 1.9, probable error 1.5 — there is at present no evidence to substantiate a four-factor hypothesis and none but this to suggest it. There are several points that sometimes make difficult the identification of aleurone color. Color is usually not well developed in seeds that are not fully matured. When *R* is heterozygous and is brought into the cross from the male parent, the seeds are usually mottled with color, but in some cases they are only faintly specked. In some strains aleurone color is much paler than in others, as if due to a dilution factor. When all these conditions are present together, it is not surprising if some seeds belonging genotypically in the colored class are counted as colorless. But none of the colorless seeds, so far as they have been tested, have given colored offspring, as would be expected if many seeds genotypically colored had been classed as colorless.

The close correspondence between observation and hypothesis, when all the sixty-one progenies (table 1) are lumped together, is of course equally apparent whether the results are stated as a percentage, as a ratio, or in the numbers actually observed. The observed percentage of colorless seeds has been stated previously as 57.79±0.21, while the expected percentage is 57.81. Against the expected ratio of 27:37, the actual ratio is 27.013:36.987±0.134. The observed and expected numbers are given below, the probable error being 53.1:

| | Colored | Colorless | Total |
|---|---|---|---|
| Observed | 10,674 | 14,615 | 25,289 |
| Calculated | 10,669 | 14,620 | 25,289 |
| Difference | —5 | +5 | 0 |

### RESULTS IN THE $F_3$ AND $F_4$ GENERATIONS

There are obviously several ways of checking these $F_2$ results and thereby the three-factor hypothesis derived from them. The first test to receive attention is naturally the behavior n $F_3$ and $F_4$.

From colorless $F_2$ seeds of the 27:37 lot (table 1) there were produced fifteen $F_3$ progenies (table 3, group 1, page 269). Two of these had only twenty individuals each and a third only forty, but the remaining progenies ranged from 240 to 770 in number of individuals. The total number of individuals was approximately 5930, all but three of which were colorless. The three colored seeds were doubtless due to foreign pollen that reached the silks accidentally. The fifteen colorless $F_2$ individuals, all that were tested, bred true colorless in $F_3$, therefore, as was expected of them.

From colored $F_2$ seeds of the 27:37 lot, eighty-eight $F_3$ progenies were counted (table 4, page 271). The number of individuals in a progeny ranged from 13 to 548, with a total of 18,864. The percentages of colorless seeds showed extreme variations of zero — true-breeding colored — and $66.7 \pm 4.7$.

Frequency distributions of these eighty-eight $F_3$ progenies are shown in figure 71, C to G, from which it is seen that they fall into three separate groups. The first group (C of figure 71 and table 4) had no colorless seeds. The second group, D, includes percentages of colorless seeds varying from $20.0 \pm 5.3$ to $28.5 \pm 1.8$, with an average of $24.5 \pm 0.5$. Evidently group D fluctuates about 25 per cent, or the 3:1 ratio. Of the deviations from 25 per cent, seven are plus and eleven are minus. No deviation is so large as twice the probable error. Six deviations are from 1 to 1.9, and twelve from 0.1 to 0.9, times the corresponding probable errors.

All the other $F_3$ progenies appear in a single group (fig. 71, E). There are definite indications, however, that this group is not a homogeneous one. There are prominent modes at classes 43 and 55. These, it will be recalled, are near the percentage of colorless individuals in 9:7 and

27:37 ratios, the theoretical percentages being 43.75 and 57.81, respectively. Apparently there is here a tendency for the $F_3$'s to collect into 9:7 and 27:37 groups, but the fluctuations are so great that the two groups are not sharply separable. If group E (fig. 71) is divided arbitrarily by a line between classes 49 and 52, groups F and G so formed can be compared with the expected 9:7 and 27:37 groups. It must be remembered, however, that the two groups cannot be correctly separated in this arbitrary way. Proof that at least two $F_3$ progenies are wrongly classed by this method is presented later in a discussion of results in $F_4$.

The percentages of group F (table 4) range from $36.4\pm2.0$ to $50.0\pm7.5$. Of the deviations from the expected 43.8 per cent, thirteen are minus, seventeen are plus, and one is zero. Eighteen of the deviations are from 0 to 0.8, nine are from 1.1 to 1.8, three are from 2.4 to 2.9, and one is 3.7, times the probable errors concerned. The average percentage of colorless individuals for the group as a whole is $44.2\pm0.4$, a deviation from expectancy barely equaling the probable error.

The percentages of group G range from $50.9\pm4.4$ to $66.7\pm4.7$. Of the deviations from the theoretical 57.8 per cent, thirteen are plus and twenty-three are minus. None is greater than 2.2 times the probable error. Fourteen deviations are from 0.2 to 0.9, twenty are from 1 to 1.9, and two are 2.2, times the respective probable errors. The average percentage of colorless individuals in the group as a whole is $57.1\pm0.4$, the deviation from the expected 57.8 per cent being 1.7 times the probable error.

It is obvious from the foregoing that, as a whole, groups D, F, and G agree fairly well with the theoretical percentages of colorless seeds in 3:1, 9:7, and 27:37 ratios. Pending further tests, therefore, the observed numbers of $F_3$ progenies of groups C, D, F, and G (table 4 and figure 71) may well be compared with the numbers expected on the basis of a 27:37 $F_2$ ratio, as follows:

| | C | D | F | G | Total |
|---|---|---|---|---|---|
| Observed | 3 | 18 | 31 | 36 | 88 |
| Calculated | 3 | 20 | 39 | 26 | 88 |
| Difference | 0 | —2 | —8 | +10 | 0 |

When it is attempted to separate arbitrarily the 9:7 group (F) from the 27:37 group (G), the fit of observed with calculated results is not

particularly good. The value of $\chi^2$ (Weldon, 1901:235, and Harris, 1912) is 5.69, and that of $P$ (Elderton, 1901, and Pearson, 1914:26–28, table XII) is 0.125, which gives odds of 7 to 1 against the observed deviations being due to chance. When, however, the two groups, F and G, are considered together as group E, there is very close agreement between observation in $F_3$ and expectation based on a 27:37 $F_2$ behavior, as is seen in the following comparison:

| | C | D | E | Total |
|---|---|---|---|---|
| Observed | 3 | 18 | 67 | 88 |
| Calculated | 3 | 20 | 65 | 88 |
| Difference | 0 | —2 | +2 | 0 |

Here $\chi^2 = 0.26$, indicating a very high value of $P$ (values of $P$ when $\chi^2$ is less than unity are not listed in Pearson's tables).

Notwithstanding the exceptionally close fit when groups F and G are lumped together as group E, there is no indication that group E is a homogeneous one, such as would be expected in $F_3$ from a 9:7 $F_2$ lot. The prominently bimodal condition of group E has been noted before and is obviously contrary to expectation in $F_3$ from 9:7 $F_2$'s. But even more definite evidence against the possibility that the $F_3$ groups C, D, and E could have been produced from a 9:7 $F_2$ is afforded by a direct comparison of observed $F_3$ numbers with numbers calculated on the basis of a 9:7 $F_2$, as follows:

| | C | D | E | Total |
|---|---|---|---|---|
| Observed | 3 | 18 | 67 | 88 |
| Calculated | 10 | 39 | 39 | 88 |
| Difference | —7 | —21 | +28 | 0 |

The value of $\chi^2$ here is 36.3. There is therefore less than one chance in a million that the observed deviations may be due to the errors of random sampling.

On the whole, then, the assumption of three heterozygous factors in $F_1$, with a consequent 27:37 $F_2$ ratio, is afforded support by the $F_3$ behavior.

This conclusion receives further support from a comparison of groups C to G, figure 71, with the data of thirty-eight $F_3$ progenies produced from the true 9:7 $F_2$'s shown in figure 71, B, and of the sixteen $F_4$ progenies from 9:7 lots of these $F_3$'s. The data for $F_3$ and $F_4$, including fifty-four progenies and 9785 individuals, are brought together in table 5 (page 274) and are shown in figure 71, H to J, in the form of frequency distributions of percentages of colorless individuals. Since the behavior of the 9:7 lots is not in question — their use here being merely for comparison with the supposed 27:37 lots — economy of time is gained and no error is involved in thus lumping together the $F_3$'s and the $F_4$'s. The distributions fall into three distinct groups, as expected: group H (table 5 and figure 71) is made up of the true-breeding colored progenies; group I has a prominent mode at 25 per cent, being made up of 3:1 progenies; group J has its mode at 43 and its mean slightly above 43 per cent, 9:7 progenies. There is no tendency in group J toward the bimodal condition seen in group E. Moreover, the numbers of progenies appearing in these groups are in almost perfect accord with expectation based on 9:7 ratios in the preceding generations ($\chi^2 = 0.21$). The comparison of observed numbers with those expected from 9:7 parents is as follows:

| | H | I | J | Total |
|---|---|---|---|---|
| Observed | 7 | 23 | 24 | 54 |
| Calculated | 6 | 24 | 24 | 54 |
| Difference | −1 | +1 | 0 | 0 |

Returning now to the 27:37 lots, it is seen that the $F_4$ progenies from each of the $F_3$ groups afford still further evidence in favor of the three-factor hypothesis. From the 3:1 lots of $F_3$ (group D of figure 71 and table 4), only six colorless and six colored individuals were tested. The six former bred true colorless (table 3, group 2), producing approximately 2010 colorless and no colored $F_4$'s. Of the six colored $F_3$'s tested in $F_4$ (table 6, page 276), one (group 1) bred true colored, having 220 colored and no colorless seeds, and five (group 2) threw colored and colorless individuals in ratios approximating 3:1, the percentages of colorless ranging from $21.2 \pm 2.1$ to $27.3 \pm 1.8$. The counts in this case totaled 1261, of which 951 were colored and 310 were colorless, an average of

24.6±0.8 per cent colorless. No other types were thrown. So far as they go, the results are therefore in accord with expectation, except that instead of one breeding true and five giving 3:1 ratios, there should theoretically have been two of the former and four of the latter.

From $F_3$ 9:7 lots only four colorless individuals were tested in $F_4$ (table 3, group 3). All bred true, with approximately 470 colorless and no colored offspring. Of the colored $F_3$'s tested, some gave 3:1 and some 9:7 ratios, as expected, but some gave undoubted 27:37 ratios. The last obviously is not in accord with the hypothesis here being tested. These individuals belonged to an $F_3$ lot with 49.1±1.8 per cent colorless seeds (pedigree 1983–36). Since, as noted earlier, the 9:7 and 27:37 $F_3$ groups were separated arbitrarily by a line between classes 49 and 52 (fig. 71, F and G), this progeny fell in the 9:7 group. The mid-point between the two groups is 50.5 per cent, or 1.4 per cent above the percentage given by the progeny in question. Since the probable error of 1.8 per cent is greater than this difference, there could of course be no certainty that this lot was correctly classed. It seems probable that it really belonged in the 27:37 rather than in the 9:7 $F_3$ class. The individuals concerned are therefore considered with the 27:37 lot discussed below. Similarly, some of the individuals classed in $F_3$ with the 27:37 group threw no 27:37 progenies in $F_4$, and are therefore classed here as having come from the 9:7 group. All these belonged to a single $F_3$ progeny (pedigree 1983–87) which had 51.2±3.0 per cent colorless seeds. Its deviation from the mid-point between the two groups (50.5 per cent) was only 0.7 per cent. Since its probable error was 3 per cent, it might well have belonged to the 9:7 rather than to the 27:37 group.

When these adjustments are made, it is found that of the seven colored individuals of the $F_3$ 9:7 group tested in $F_4$ none bred true, whereas one in nine was expected to do so. Four gave 3:1 ratios in $F_4$, with percentages of colorless varying from 22.1±3.5 to 29.2±1.8 and an average of 25.9±1.0 (table 6, group 3); the other three gave 9:7 ratios, with from 42.6±2.4 to 49.5±3.2 per cent colorless and an average of 45.9±1.7 (group 4). Theoretically the seven colored $F_3$'s should have given in $F_4$ true-breeding, 3:1, and 9:7 progenies in the numerical relation of 1:3:3, whereas the observed relation was 0:4:3, a close approximation for the small numbers involved ($\chi^2 = 1.33$ and $P = 0.53$).

Finally, of the 27:37 $F_3$ lots (with corrections as noted above), there were tested in $F_4$ fifteen colorless and twenty-six colored individuals (tables 3 and 6). All the fifteen colorless bred true, with total offspring approximating 3250 colorless and 1 colored individuals (table 3, group 4), the latter doubtless an accident. Of the twenty-six colored $F_3$'s tested, two bred true with a total of 358 colored and no colorless offspring (table 6, group 5); six $F_3$'s gave colored and colorless offspring in approximately 3:1 ratios, the percentages of colorless running from $23.6\pm1.5$ to $27.5\pm1.7$ with an average of $25.9\pm0.6$ (group 6); eleven $F_3$'s threw 9:7 ratios with percentages varying from $38.8\pm4.8$ to $47.5\pm4.4$ (group 7). The last-named group totaled 2638, of which 1456 were colored and 1182 were white — an average of $44.8\pm0.7$ per cent colorless. Seven $F_3$'s gave 27:37 ratios in $F_4$, with percentages of colorless ranging from $54.9\pm2.9$ to $65.2\pm2.7$ (group 8). In this group there were 607 colored and 875 colorless individuals, or a total of 1482, with $59.0\pm0.9$ as an average percentage of colorless. On the whole, therefore, the 27:37 group of $F_3$'s gave $F_4$ results in remarkably close accord with expectation, considering the small numbers of progenies involved. The fifteen white $F_3$'s bred true; the twenty-six colored ones threw true-breeding, 3:1, 9:7, and 27:37 groups in the relation of 2:6:11:7, whereas 1:6:12:8 is the theoretical grouping for a total of twenty-seven.

Since these twenty-six $F_4$ lots came from colored seeds of 27:37 $F_3$'s, they can legitimately be added to the eighty-eight $F_3$ lots that came from colored seeds of 27:37 $F_2$'s (table 4). The one hundred and fourteen progenies, totaling 25,546 individuals, were distributed among true-breeding, 3:1, 9:7, and 27:37 groups in the relation of 5:24:42:43, whereas the theoretical distribution is 4:25:51:34. The odds against the occurrence by chance of deviations so great as this are about 3.2 to 1 ($\chi^2 = 4.26$ and $P = 0.239$). This is not a bad fit when it is recalled that the line arbitrarily drawn between the overlapping 9:7 and 27:37 groups has been shown not to separate the two groups accurately. When the 9:7 and 27:37 groups of this stock are thrown together there is almost perfect agreement between observation and hypothesis ($\chi^2 = 0.29$), the observed distribution into the three groups being 5:24:85 and the theoretical 4:25:85.

Aside from the obviously heterogeneous nature of the third group, as constituted above, in 27:37 stocks, and the apparent homogeneity of

the third group in 9:7 stocks, nothing could separate the two stocks more sharply than the relative numbers of progenies distributed to the three groups. For this comparison the one hundred and fourteen $F_3$ and $F_4$ progenies of the 27:37 stock discussed above, and the fifty-four $F_3$ and $F_4$ progenies of the 9:7 stock considered earlier (page 240), may be used. To make the comparison the more readily, the one hundred and fourteen progenies of the 27:37 stock and the fifty-four progenies of the 9:7 stock have been reduced to the common basis of one hundred. Each group of either stock, stated thus as a percentage of all the progenies of that stock, is given below together with the theoretical percentages:

| Stock | Percentage of total progenies | | | |
|---|---|---|---|---|
| | First group | Second group | Third group | Total |
| 9:7 stock | | | | |
| Observed | 12.9 | 42.6 | 44.5 | 100 |
| Calculated | 11.1+ | 44.4+ | 44.4+ | 100 |
| 27:37 stock | | | | |
| Observed | 4.4 | 21.0 | 74.6 | 100 |
| Calculated | 3.7 | 22.2 | 74.1 | 100 |

## THE GENETIC CONSTITUTION OF COLORLESS SEGREGATES

The foregoing account of tests of the three-factor hypothesis of aleurone color has had to do almost wholly with progenies derived from colored $F_2$ and $F_3$ individuals, and the results have been found to be in close agreement with the hypothesis The only tests so far reported of the colorless individuals of any generation are their true breeding in later generations. While this is in accord with the three-factor hypothesis, it is, of course, equally in keeping with a two-factor or even a one-factor hypothesis. None the less, white segregates from supposed 27:37 lots afford the most nearly crucial test of the hypothesis.

It is well known that the seven colorless individuals of any 9:7 progeny previously investigated consist of three types, namely, *C r*, *c R*, and *c r*. Similarly, among the thirty-seven colorless individuals of a 27:37 ratio, there should be found seven types, as follows: *a C R*, *A c R*, *A C r*, *A c r*,

*a C r*, *a c R*, and *a c r*. If more than three types are found, the fact constitutes positive proof against a two-factor interpretation. If all seven types can be demonstrated, the result, when taken in connection with the evidence from the behavior of the colored $F_2$'s, is little if any short of positive proof of the presence of three factor pairs. Evidence of the existence of these seven kinds of colorless aleurone is now to be presented.

*Aleurone color testers*

Three of the above-mentioned seven types of colorless aleurone — *a C R*, *A c R*, and *A C r* — are now well known to the writer and in fact are in constant use by him and his students as "aleurone color testers." These testers have been named for the recessive factor present, and are therefore known, respectively, as *A* testers, *C* testers, and *R* testers.

That each of these testers has a single recessive factor pair is shown by the $F_2$ generation of crosses between them and types with homozgyous colored aleurone. The records of such crosses are given in table 7 (page 278). The ratios thruout approximate 3:1. Thus, the percentages of colorless individuals in nine $F_2$ progenies of crosses involving the *A* tester (group 1) range from $20.6\pm1.5$ to $25.9\pm1.7$, with an average of $23.8\pm0.5$ for the 3630 individuals concerned; crosses involving the *C* tester (group 2) range in percentage of colorless individuals from $22.6\pm1.7$ to $30.3\pm1.5$, with an average of $25.6\pm0.5$ for the 3595 individuals of the ten $F_2$ progenies; while the fourteen $F_2$ progenies from crosses involving the *R* tester (group 3) exhibit percentages of colorless individuals of from $20.6\pm1.6$ to $30.4\pm1.5$, with an average of $27.0\pm0.4$ for the 5337 individuals. Taken together, the thirty-three $F_2$ progenies, with a total of 12,562 individuals, give an average of $25.7\pm0.3$ per cent colorless.

That these three lots of aleurone testers are genetically distinct, each with a different recessive factor pair from either of the other two, is shown by the $F_1$ and $F_2$ results of intercrosses between the three types. Reciprocal intercrosses between the three testers should, if the three-factor hypothesis is correct, give in $F_1$ the results indicated in the following diagram:

| | *a C R* | *A c R* | *A C r* |
|---|---|---|---|
| *a C R* | Colorless | **Colored** | **Colored** |
| *A c R* | **Colored** | Colorless | **Colored** |
| *A C r* | **Colored** | **Colored** | Colorless |

The observed results in $F_1$ of numerous crosses between the three aleurone testers are presented in table 8 (page 279). Except for a few individuals, doubtless due to the effect of a few grains of stray pollen that reached the silks accidentally, the results are in exact accord with expectation as indicated in the preceding diagram. Thus, intercrosses of like testers gave colorless $F_1$'s, while crosses of unlike testers gave colored $F_1$'s, as detailed below.

Seven crosses of *A* testers by *A* testers (table 8, group 1) gave approximately[5] 1890 colorless seeds and only 1 colored, the latter doubtless due to accidental pollination; nine crosses of *C* testers with *C* testers (group 2) yielded about 2360 colorless and only 4 colored seeds; fourteen crosses of *R* testers by *R* testers (group 3) produced about 3900 colorless and no colored seeds. On the other hand, twelve crosses of *A* testers by *C* testers and reciprocals (group 4) gave about 4440 colored seeds and only 7 colorless ones; eleven crosses of *A* testers by *R* testers and reciprocals (group 5) yielded approximately 3670 colored and only 6 colorless seeds; twenty-nine crosses of *C* testers by *R* testers and reciprocals (group 6) resulted in about 7170 colored and only 9 colorless seeds. In summary, thirty crosses of like aleurone testers gave 8150 colorless and 5 colored seeds, while fifty-two crosses between unlike testers gave 15,280 colored and 22 colorless seeds. The off-type seeds, numbering 27 to 23,430 type seeds, or only slightly more than one-tenth of one per cent, are, the writer is convinced, largely due to accidents in pollination, a difficulty he has never been able entirely to overcome.

Crosses between any two of these aleurone testers that result in colored $F_1$ individuals should, if the three-factor hypothesis holds, give 9:7 ratios in $F_2$. A few such $F_2$ results are recorded in table 9 (page 282). Five progenies of *A* testers crossed by *C* testers (table 9, group 1) gave percentages of colorless ranging from $39.5\pm2.4$ to $44.7\pm2.1$, with an average of $42.2\pm0.7$ for the 1995 individuals; five progenies of *A* testers by *R* testers (group 2) gave percentages of colorless ranging from $40.3\pm1.5$ to $46.8\pm1.5$, with an average of $44.0\pm0.7$ for the 2079 individuals; four progenies of *C* testers by *R* testers (group 3) gave percentages of colorless ranging from $43.2\pm5.5$ to $48.9\pm2.5$, with an average of $45.4\pm1.1$ for the 886 individuals. The general average for the fourteen $F_2$ progenies with a total of 4960 individuals is $43.7\pm0.4$ per cent colorless, or almost

[5] The numbers were recorded to the ten nearest the product of the number of rows of seeds and the number of seeds in one row.

exactly the expected percentage of 43.75. While some of the individual deviations from 9:7 ratios are rather large, in no case is a deviation more than 2.3 times the probable error. On the whole, therefore, the results are believed to be quite in agreement with expectation.

*Other classes of colorless aleurone*

With the three colorless aleurone testers, *a C R*, *A c R*, and *A C r*, positively identified, it becomes possible by their use to identify other classes of colorless aleurone. The available evidence of the existence of other colorless types has been brought together in table 10 (page 283) and is discussed below.

The evidence (table 10, group 1) indicates that family 6880 has the genetic constitution *A c r*. The evidence for the presence of *A*, so far as it is given in the table, is based on only 10 individuals, the cross of 6880–3 with an *A* tester having resulted in 10 colored and no colorless seeds. What the writer regards as conclusive evidence for the presence of *A* is the fact, not shown in the table, that the plant bearing this ear — as well as its sibs and its selfed parent — developed considerable red pigment in the sheaths, tassel, silks, and other parts, a condition never observed in an *a a* plant. In fact, the symbol *A* was first used to represent a gene for the development of a reddish anthocyanic pigment in these parts of the plant, and was only later found also to be a factor in aleurone color development. The evidence for this interpretation is reserved for publication in another paper. The evidence that family 6880 is *c c r r* is clear, since a cross with a *C* tester and three crosses with *R* testers gave uniformly colorless seeds.

Families 6881 and 7531 (table 10, group 2) are undoubtedly *a C r* in constitution. Crosses with *C* testers gave only colored seeds, and crosses with *A* and *R* testers only colorless seeds, except for two off-type seeds accounted for as due to accidental pollinations.

Families 7525 and 7526 (table 10, group 3) are shown to be *c R* in constitution, crosses with *C* testers having given colorless seeds and with *R* testers colored seeds, except for two seeds doubtless due to accident. The evidence for the *a a* condition is in line with what was said above for the presence of *A* in family 6880. Families 7525 and 7526 and their parents were wholly lacking in anthocyanic pigment. These families are therefore properly regarded as *a c R*.

Family 6885 (table 10, group 4) is shown with a high degree of certainty to be *a c r*. Except for a single accidentally pollinated seed, the two crosses with *A* testers, the three crosses with *C* testers, and the five crosses with *R* testers gave only colorless seeds.

It is believed that the evidence recorded above approximates closely a demonstration of the existence of the seven classes of colorless aleurone, *a C R*, *A c R*, *A C r*, *A c r*, *a C r*, *a c R*, and *a c r*, expected on the hypothesis presented early in this paper. It must be pointed out, however, that not all of these types have as yet been found in an $F_2$ progeny giving a 27:37 ratio. Some of them have come directly from such progenies, but others have been found in quite unrelated cultures. It is interesting to note that the common varieties of dent, flint, and sweet corn lacking aleurone color are *r r* — that is, they lack the *R* factor; while all the varieties known to the writer, except a single variety of dent corn, are *A A*. There is apparently greater diversity with respect to the *C* factor. Some are apparently *C C*, thus constituting *R* testers provided they are also *i i*, while some are, at least in part, *c c*, and others have *C c* individuals. Some colorless pop corns are *R R* and, since all apparently are *A A*, they are *C* testers. Of course the varieties with colored aleurone, notably certain varieties of pop, sweet, and flour corn, are *A C R*. It is interesting to note that at least some samples of teosinte (*Euchlaena mexicana* Schrad.), which is thought by some to be distantly related to *Zea mays* L. and which is known to hybridize with it, lack aleurone color. What aleurone color factors teosinte has, if any, is as yet unknown.

### EXAMPLES OF GENOTYPES INVOLVING *A*, *C*, AND *R*

While the direct evidence already presented is the best demonstration, and perhaps the only one needed, of the existence of the expected classes of colored and colorless aleurone involving only *A*, *C*, and *R*, there has naturally accumulated, during the eight or nine years since the writer began his studies of aleurone color, a bulky mass of less direct but consistent evidence. Many of the accumulated data could not be interpreted until, after numerous failures and some partial successes — the latter, thru misunderstanding and too hasty application of them, often proving quite as perplexing as the failures — the three aleurone testers were finally isolated and tested as outlined earlier in this account. There is obviously no need of burdening the reader with all or even with any considerable part of this accumulated evidence. It seems desirable,

however, to note here a few bits of further evidence to serve merely as a sample of the whole.

Family 6881, for instance, was shown (table 10, group 2) to be *a C r*, and a cross of an individual (no. 3) of this family with a *C* tester, *A c R*, (6856–24) is seen to have given in $F_1$ colored seeds only. The $F_2$ generation of this cross should show a 27:37 ratio of colored to colorless individuals. Similarly, family 6885 (group 4) was shown to be *a c r*. Crosses of 6885 with several lots of homozygous colored aleurone gave colored $F_1$'s. Here also 27:37 ratios are to be expected in $F_2$. The results are given in table 11 (page 284). The percentages of colorless seeds for the seven crosses ranged from 55.3±1.3 to 60.2±2.3, with an average of 57.2±0.6 whereas the theoretical percentage is 57.8.

The $F_1$ lots that gave the above results on being selfed, were also crossed with aleurone testers and with family 7520, which came from self-pollinated plants of 6885 shown to be *a c r* (table 10, group 4). The records of these crosses are presented in table 12 (page 284). Plants of the genotype *A a C c R r* should give 1:1 ratios of colored to colorless when crossed with either of the aleurone testers, and 1:7 ratios when crossed with *a c r*. Two crosses with *A* testers, *a C R*, gave an average of 50.1±1.0 per cent colorless (table 12, group 1); three crosses with *C* testers, *A c R*, gave an average of 50.6±0.9 (group 2); and three crosses with *R* testers, *A C r*, gave an average of 50.1±1.0 (group 3). Four crosses with *a c r* gave an average of 86.8±0.5 per cent colorless (group 4), 87.5 being the percentage equivalent to a 1:7 ratio.

In contrast with the results shown in table 12, similar crosses with plants of a different genotype are reported in table 13 (page 285). The plants thus crossed were themselves crosses of *C* testers with *R* testers and were therefore *A A C c R r*. The $F_2$ progenies of these crosses, so far as noted, gave 9:7 ratios of colored to colorless (table 9, group 3), as was expected. When the $F_1$ plants, *A A C c R r*, were crossed with *C* and *R* testers (table 13, groups 2 and 3), the average percentages of colorless seeds were 50.9±1.1 and 50.0±0.8, respectively, just as in the case of similar crosses of *C* and *R* testers with *A a C c R r* (table 12). But when crossed with an *A* tester (table 13, group 1), all the seeds were colored, as expected; and when crossed with *a c r* (table 13, group 4), 71.7±1.3 per cent were colorless, whereas 75 per cent were expected. The expected results were therefore approximated, both from selfing and from crossing, for *A a C c R r* and *A A C c R r*, as shown in the following diagram:

| | Selfed | Crossed with | | | |
|---|---|---|---|---|---|
| | | *aaCCRR* | *AAccRR* | *AACCrr* | *aaccrr* |
| *AaCcRr* | 27:37 | 1:1 | 1:1 | 1:1 | 1:7 |
| *AACcRr* | 9:7 | 1:0 | 1:1 | 1:1 | 1:3 |

The examples given in the preceding paragraphs illustrate how it is possible to use the three aluerone testers in order to determine the genotype, with respect to the factors *A*, *C*, and *R*, of any lot of maize, provided

| Possible genotypes | *A* tester *aaCCRR* | *C* tester *AAccRR* | *R* tester *AACCrr* |
|---|---|---|---|
| *AACCRR* | 1:0 | 1:0 | 1:0 |
| *AaCCRR* | 1:1 | 1:0 | 1:0 |
| *AACcRR* | 1:0 | 1:1 | 1:0 |
| *AACCRr* | 1:0 | 1:0 | 1:1 |
| *AACcRr* | 1:0 | 1:1 | 1:1 |
| *AaCCRr* | 1:1 | 1:0 | 1:1 |
| *AaCcRR* | 1:1 | 1:1 | 1:0 |
| *AaCcRr* | 1:1 | 1:1 | 1:1 |
| *aaCCRR* | 0:1 | 1:0 | 1:0 |
| *aaCcRR* | 0:1 | 1:1 | 1:0 |
| *aaCCRr* | 0:1 | 1:0 | 1:1 |
| *aaCcRr* | 0:1 | 1:1 | 1:1 |
| *AAccRR* | 1:0 | 0:1 | 1:0 |
| *AaccRR* | 1:1 | 0:1 | 1:0 |
| *AAccRr* | 1:0 | 0:1 | 1:1 |
| *AaccRr* | 1:1 | 0:1 | 1:1 |
| *AACCrr* | 1:0 | 1:0 | 0:1 |
| *AaCCrr* | 1:1 | 1:0 | 0:1 |
| *AACcrr* | 1:0 | 1:1 | 0:1 |
| *AaCcrr* | 1:1 | 1:1 | 0:1 |
| *AAccrr* | 1:0 | 0:1 | 0:1 |
| *Aaccrr* | 1:1 | 0:1 | 0:1 |
| *aaCCrr* | 0:1 | 1:0 | 0:1 |
| *aaCcrr* | 0:1 | 1:1 | 0:1 |
| *aaccRR* | 0:1 | 0:1 | 1:0 |
| *aaccRr* | 0:1 | 0:1 | 1:1 |
| *aaccrr* | 0:1 | 0:1 | 0:1 |

*I* is not concerned. In fact, these testers are in common use for this purpose by the writer and his students. For the convenience of others who may desire to use them, there is presented in the preceding dia-

gram the theoretical behavior of all the twenty-seven possible genotypes involving only *A*, *C*, and *R*. It should be understood that not all the genotypes included in the diagram have been actually demonstrated.

## OTHER FACTORS INFLUENCING ALEURONE COLOR

In this paper the writer has dealt primarily with the three factor pairs, *A a*, *C c*, and *R r*. Mention has also been made of the pairs *I i* and *Pr pr*. It should be noted that these five are not the only genetic factors involved in aleurone color, and moreover that aleurone-color development is influenced by certain non-genetic factors.

### *Non-genetic factors*

Anyone who has given attention to the inheritance of aleurone color in maize must have noted, in addition to the more or less sharp segregation of colored and colorless seeds, a wide variation in the quality and intensity of the color produced. Some of these variations have been noted by East and Hayes (1911), by the writer (Emerson, 1911), and particularly by Harper.[6] It is the writer's experience that the development of aleurone color is usually influenced noticeably by the degree of maturity of the seeds, and that its appearance is affected by the composition and color of the underlying endosperm. It is true that aleurone color begins development in very immature seeds, but its intensity is greatly weakened by immaturity. The purple color of aleurone tends to be bluish or light purplish in immature seeds, while in some cases it is almost black in fully mature seeds. With certain rather late-maturing strains in the short seasons of Ithaca, New York, it is often necessary to harvest ears from immature plants that have been killed by frost. It has been found that with slow drying of such ears the aleurone color develops fairly well, while rapid drying interferes seriously with color development. Even when well developed, the appearance of aleurone color, particularly of the lighter colors, is markedly influenced by the color of the underlying endosperm. Over white endosperm the colors are clear, while over yellow the reds and the purples appear brown, and light bluish purple shows as a distinct green. Since on an ear that is heterozygous for yellow

[6] Papers on aleurone color were presented by Dr. R. A. Harper before the Botanical Society of America at its winter meetings of 1915–16 and 1916–17. These papers have not been published. A brief abstract of the first paper appeared in volume 43 (1916) of Science, on page 290.

endosperm there may be all gradations from clear white to deep yellow, the apparent variation in aleurone color is confusing. Moreover, the composition of the endosperm is not without its influence on the appearance of the aleurone color. Medium strong purple aleurone usually seems lighter over corneous and darker over sugary endosperm. Over waxy and floury endosperm, strong purple appears as a dull black.

*Genetic factors*

It is not intended to suggest that variations in maturity or in the color, composition, or texture of the underlying endosperm can be made to account for all the variations of aleurone color. There are certainly definite genetic differences between aleurone colors. The difference between ordinary purple and red aleurone is well known (East and Hayes, 1911, and Emerson, 1911) to be due to the factor pair *Pr pr*. In some of the writer's cultures a dominant dilution factor — or a recessive intensifier — is known to behave as a simple Mendelian unit. There are also bluish purples contrasted with reddish purples where the difference is apparently not due to the *Pr pr* pair, but the genetic behavior of these colors is not as yet fully understood.

In addition to the differences in color, there are in the writer's cultures three well-marked color patterns — self-color, speckled, and dark-capped. Speckled seeds are common in some varieties of flour corn grown in the West. The dark-capped type is grown by various Indian tribes of the Southwest and also by certain tribes of the northern plains region. The color in the seeds of these types is confined to the crown of the seed, and varies from a mere speck at the point of attachment of the silk to a large spot covering the whole crown or even extending part way down the sides of the seed. Both the speckled and the dark-capped patterns are apparently simple recessives to self-color. A third pattern has been shown the writer by Messrs. Collins and Kempton, who also have studied the two patterns noted above. The third pattern is the reverse of the dark-capped type in that the color covers the sides of the seeds, leaving a colorless spot of variable size at the crown. Another pattern, known to the writer as blotched, or smudged, is apparently distinct from the speckled pattern. This has not been fully studied, but seems to be related to the *C* factor. Finally, there is the mottling, or speckling, that is often seen in heterozygous colored aleurone.

### RELATION OF THE *R* FACTOR TO MOTTLING

East and Hayes (1911:74) call attention to the fact that mottled seeds are heterozygous. They state: "Some unknown cause produces many seeds in this cross that are heavily splashed with purple. These always behaved as heterozygous purples, although the heterozygous purples were not always splashed, but were generally full colored purples."

The writer has been able to show that this mottling of heterozygous seeds is definitely associated with the *R r* factor pair. Collins and Kempton have informed the writer that they also have given attention to this matter and have reached the same conclusion. Records of $F_2$ and $F_3$ progenies from an $F_1$ of the genotype *A A C C R r* are given in table 14 (page 286). While considerable variation in the percentage of colorless seeds in the heterozygous families (groups 1, 2, and 3) is manifest, there is on the whole fair agreement with the 25 per cent of colorless seeds expected where a single one of the three factor pairs *A a*, *C c*, and *R r* is heterozygous. That the *R r* pair is the one concerned is shown by crosses of aleurone testers with plants of families recorded in table 14. The results of these crosses are presented in table 15 (page 287). The three crosses with *C* testers, *A c R* (table 15, group 1) gave only colored seeds, thus showing that *C* was not heterozygous. The testers employed for the crosses recorded in groups 2 and 3 were thought, when the crosses were made, to be *R* testers, *A C r*, but were later found to be *a C r*. They nevertheless serve here for *R* testers, because the plants with which they were crossed were known to be *A A*. One parent of the original cross, from which the $F_2$'s of table 14 came, was homozygous for colored aleurone and therefore must have been *A A*; the other parent, tho with colorless aleurone, was homozygous for red color in sheath, husks, tassel, silks, and other parts, a condition never seen except in *A A* plants. The crosses with *a C r* (groups 2 and 3) gave both colored and colorless offspring. The percentage of colorless varied greatly, doubtless due to the very small numbers involved; but the total of 109 individuals comprised 56 colored and 53 colorless, which is not far from the expected 50 per cent of colorless.

Similar evidence is afforded by the records given in groups 4, 5, and 6 of table 15. The $F_3$ progenies of the colorless $F_2$ individuals of table 14, group 1, tho not recorded in that table, were all colorless as expected. Crosses of these colorless lots with *C* testers, *A c R* (table 15, groups 4 and

5), gave all colored seeds, just as was true of group 1, thus showing again the *C C* condition. Crosses with *a C r* (group 6) gave only colorless seeds, indicating the *r r* condition. Further evidence that the *R r* pair is the one concerned in mottling is given in connection with data presented later in this paper (page 255).

The percentage of mottled seeds in the heterozygous families of table 14 (groups 1, 2, and 3) varies considerably, the average of all being $30.1 \pm 0.8$ per cent mottled in a total of 2005 colored individuals. From considerations noted later (page 254), the theoretical percentage is taken as 33.3. In only three of the families is there a plus deviation from 33.3 per cent. Since some of the seeds recorded as mottled were only slightly so, it seems possible that some which were recorded as self-colored might have been very inconspicuously mottled.

The $F_2$ results are shown in group 1 of table 14, and the $F_3$ results in groups 2, 3, and 4. The cultures recorded in group 2 came from mottled $F_2$ seeds of group 1, and those given in groups 3 and 4 from self-colored seeds of group 1. It is noteworthy that the percentage of mottled seeds in $F_3$ was quite as great from self-colored (group 3) as from mottled (group 2) $F_2$ seeds. The important consideration, however, is that of the eight mottled $F_2$ individuals tested in $F_3$ (group 2), all were heterozygous with respect to color, while of the sixteen self-colored $F_2$ individuals, ten (group 3) were heterozygous and six (group 4) were homozygous. Moreover, all the progenies from homozygous colored seeds (group 4) were self-colored thruout. So far as they go, then, the data are in accord with the results of East and Hayes (1911). The $F_3$ data recorded in table 14 include only such families as were sorted into mottled and self-colored. There were actually observed a total of forty-seven $F_3$ progenies from mottled $F_2$ seeds, all of which had both colored and colorless individuals, and eighty-four $F_3$ progenies from self-colored $F_2$ seeds, of which fifty-two had both colored and colorless and thirty-two had only colored individuals. Every mottled $F_2$ seed, therefore, so far as tested, proved to be heterozygous, while of the self-colored $F_2$ seeds tested about five-eighths were heterozygous and three-eighths were homozygous. If, as expected, one-third of the colored seeds had been mottled and two-thirds self-colored, and if all mottled seeds are heterozygous, one-half of the self-colored $F_2$ seeds should have bred true colored, whereas only about three-eighths were actually observed to do so. But

only about 28 per cent, instead of 33.3 per cent, of the $F_2$ colored seeds were recorded as mottled. Of 72 self-colored seeds to 100 colored, therefore, there should have been about 33 homozygous and 39 heterozygous. In short, about 46 per cent of the self-colored seeds should have been homozygous, as against about 38 per cent that were actually found to be so.

The hypothesis on which is based the expectancy of 33.3 per cent of mottled individuals among colored seeds, is that mottling appears only when *R* is furnished by the sperm and *r* by the egg, not when the egg is *R* and the sperm *r*. Owing to what is commonly termed double fertilization, the endosperm of maize is presumably triplex in its genetic constitution. If the maternal element contributes *R* and the paternal element *r*, the polar nuclei being *R R* and the second generative nucleus *r*, the endosperm will be *R R r*, while in the reciprocal fertilization it will be *r r R*. It is assumed that *R R r* ordinarily insures self-color, while *r r R* usually results in mottling. A plant of the genotype *R r* will, then, on self-pollination, produce seeds with the endosperm constituted as follows:

| Second generative nucleus | | *R* | *r* |
|---|---|---|---|
| Polar nuclei | *R R* | *R R R* | *R R r* |
| | *r r* | *r r R* | *r r r* |

Of any four seeds, therefore, on the average, three should be colored; and of these, two should be self-colored, *R R R* and *R R r*, and one mottled, *r r R*. Moreover, of the mottled seeds all should be heterozygous, and of the self-colored seeds one-half should be heterozygous and one-half homozygous for color.

This hypothesis agrees fairly well with the results reported in table 14 and discussed above. Additional evidence is afforded by the data in table 15. When *A A c c R R* is used as the male parent, and *A A C C R r* as the female parent of a cross (table 15, group 1), approximately 50 per cent of the resulting seeds are self-colored and 50 per cent are mottled. The self-colored seeds are assumed to have received *R R* from the mother and *R* from the father, while the mottled seeds are supposed to have had *r r* from the mother and *R* from the father; the self-colored seeds, therefore, being *R R R* and the mottled ones *r r R*. When the female parent is colorless, *A A C C r r*, and the male parent is colorless, *A A c c R R*

(group 4), all the resulting seeds are mottled, *r r R*, while in the reciprocal cross (group 5) all are self-colored, *R R r*. Again, when *A A C C R r* is the female parent and *a a C C r r* the male parent (group 2), all the colored seeds are self, *R R r*, the colorless ones being obviously *r r r*. But in the reciprocal cross (group 3), all the colored seeds are mottled, *r r R*.

Obviously the most direct evidence that *R r*, rather than *A a* or *C c*, is the factor pair concerned in mottling, and that mottling is associated with the *r r R* condition, not the *R R r*, should be afforded by reciprocal crosses of aleurone testers with types having homozygous colored aleurone. Crosses of this kind are listed in table 16 (page 288). That the colored parents of these crosses were homozygous is shown by the records in group 1 of the table. Ten selfed ears had a total of 2560 seeds, all of which were self-colored. The data recorded in groups 2 to 7 of the table are from crosses of representatives of these or similar homozygous lots with aleurone testers. The *A* tester, *a C R*, was used as the female parent of three crosses (group 2), producing a total of 1460 seeds, all self-colored. As the male parent of six crosses (group 3) it gave 1700 self-colored seeds. The *C* tester, *A c R*, produced 2110 self-colored seeds from eight crosses when used as the female parent (group 4), and 1560 self-colored seeds from six crosses when used as the male parent (group 5). The *R* tester, *A C r*, when used as the male parent of five crosses (group 7), behaved exactly as did the other testers when used as either male or female parent, producing a total of 1020 self-colored seeds. But when the *R* tester was used as the female parent (group 6), wholly different results were obtained. In this case, all of the 2190 seeds of the nine crosses were mottled with color. The foregoing evidence seems to establish conclusively the fact that mottled aleurone is ordinarily produced only when *R* enters the combination from the male side, thus giving rise to the *r r R* condition of the aleurone.

An explanation of this behavior is not readily formulated. It seems likely that it is related to the behavior of corneous and floury endosperm (Hayes and East, 1915), but there is a distinct difference between the two. When corneous endosperm is crossed reciprocally with floury, the resulting endosperm is always like that of the female parent, never like the male. Here the duplex condition of either corneous or floury evidently dominates completely over the simplex condition of the other. With

respect to aleurone color, likewise, duplex *R* is apparently fully dominant over simplex *r*, but duplex *r* is not fully dominant over simplex *R*. Simplex *R* produces a definite effect even in the presence of *r r*, perhaps with the help of *r r*. A noteworthy fact in this connection is that the mottling consists of irregular patches of colorless aleurone mingled with apparently fully colored patches. Why the *r r R* condition should bring about strong color development in certain groups of cells and fail to do so in other groups, is not apparent. But the same can be said as well of definite "pattern" factors.

Attention should be called to the fact that when a very immature ear of a variety with colored aleurone is dried rapidly, the aleurone color is often irregular in its appearance. Fairly uniform color may show at the crown of the seed, with the sides colorless. The two areas are not usually sharply delimited but rather grade into each other, and the boundary region is not infrequently marked with intermingled specks or spots of colored and colorless aleurone. While this spotting would rarely if ever be mistaken for true mottling, it indicates that under certain conditions, even with homozygous colored aleurone, the color may develop more strongly or more rapidly in certain cells than in adjoining cells. Perhaps heterozygous mottling is due to the fact that the balance is so even between *R* and *r r* that chance plays an important part in determining whether or not color shall develop.

It should be recalled that speckled aleurone, characteristic of certain varieties of maize, is a simple Mendelian recessive to self-color. In general, speckling differs from mottling in being a finer pattern, but mottling varies so much in appearance that it would probably be impossible in most cases to separate mottled from speckled seeds if the two were mixed. The fact that *R* is thought to belong to a multiple allelomorphic series in its relation to color of silks, anthers, and other plant parts, suggests at once the possibility that the same may be true with respect to aleurone color. As yet, however, the writer has no definite evidence that *R* is in any way related to the speckling factor. Not only do the heterozygous mottled seeds of a single ear differ considerably in appearance, but the mottling of some ears is markedly different from that of others. Moreover, thruout certain cultures the heterozygous mottling is consistently different from that of other cultures; in some the color is so strongly developed that it might pass for self-color on hasty observation, while in

others it shows as comparatively small spots on an apparently colorless background. Whether this difference is due to a series of multiple allelomorphs of *R* or to some factor closely associated with it, it is doubtless of a genetic nature.

There is still another suggestion which may not well be overlooked. Mottling may be similar to variegation. The writer (Emerson, 1914 and 1917) has been able to show with some degree of plausibility that the variegated pattern of the maize pericarp is characterized by genetic changes at least analogous to mutations. It appears further that ordinarily only one member of a factor pair thus mutates at a given time. If the *R* factor were similar to the pericarp factor in these respects, heterozygous mottling would have a ready explanation. If *R* mutates frequently to *r*, or to some allelomorph which like *r* is not capable of acting with *A* and *C* to produce color, homozygous color, *R R R*, or even heterozygous color of the nature of *R R r*, would not be expected to change frequently to the colorless condition. A single mutation of *R R R* or *R R r* would give *R R r* or *R r r*, respectively, and color would be expected to develop. In heterozygous aleurone of the *r r R* type, however, the colorless condition must result at once if *R* changes to *r* thereby giving *r r r*. But it would seem likely that, owing to the frequency of the mutation — if indeed it is a matter of mutation — even *R R R* aleurone should sometimes become colorless thru a triple mutation, a thing not yet observed.

### ANOMALOUS COLORED-COLORLESS ALEURONE

Whether or not there is any merit in the suggestion that mottling may be due to mutational changes of the *R* factor, as noted above, there is a kind of behavior of aleurone color that is readily accounted for in that way. In crosses between colored and colorless races, occasional seeds have perhaps half of their aleurone strongly colored and half wholly colorless, or one-fourth colored and three-fourths colorless, or divided in other proportions. The line of demarcation between the colored and the colorless areas is always sharp, tho it may be somewhat irregular in outline. In an earlier paper (Emerson, 1915) the writer described a seed somewhat over half of which was colored and the remainder colorless. The seed resulted from a cross of a plant of the genotype *A A C C r r* with pollen of *A A c c R R*. The aleurone is assumed, therefore, to have been

*A A A C C c r r R*. All the seeds, except the one mentioned, were colored thruout or very indistinctly mottled. It was suggested that the anomalous seed was due to a mutation of *R* to *r* at an early division of the endosperm nucleus, so that the resulting aleurone consisted in part of *r r R* and in part of *r r r*. It is perhaps possible that such a change may have occurred in *C*, resulting in the two parts of the aleurone being *C C c* and *c c c*; but this would have necessitated a double mutation, one for each of the two *C* factors.

While it cannot be said that such anomalous seeds never occur when *R* alone is heterozygous, the writer is unable to report with certainty a single case of the kind. If they ever occur, therefore, they are certainly very rare. Such seeds have occurred occasionally when *C* or *A* alone was known to be heterozygous. For instance, in group 2 of table 7 are recorded the $F_2$ progenies of crosses in which *C* alone was heterozygous. Of the 2674 colored seeds of ten ears, five seeds, on two ears, were part colored and part colorless. Of the 3894 colored seeds of fourteen ears in which *R* alone was heterozygous (group 3), no anomalous seeds were noted. Where *A* alone was heterozygous (group 1), two colored-colorless seeds were found out of a total of 2767 colored seeds from nine ears. Similarly, of the $F_2$ progenies recorded in table 9, where in each case two factor pairs were heterozygous, no anomalous seeds were observed among the 475 colored seeds from *A A C c R r* parents (group 3) or among the 1165 colored seeds from *A a C C R r* parents (group 2), while among the 1153 colored seeds from *A a C c R R* parents (group 1) five such seeds appeared.

In crosses in which only one factor pair is heterozygous and in which the contribution of each parent is positively known, anomalous seeds occur only when the dominant factor concerned enters the cross from the male parent, and apparently never in the reciprocal cross. Thus, of the crosses recorded in table 16, where in each case one parent was homozygous colored, of the three ears of group 2 (*a C R* x *A C R*), with a total of 1460 colored seeds, two had each a single colored-colorless seed; while of the six ears of group 3 (*A C R* x *a C R*), with 1700 colored seeds, none had such a seed. In none of the other crosses listed in this table, where either *C* or *R* was alone heterozygous, involving a total of twenty-eight ears and 6880 colored seeds, were any anomalous seeds observed. In crosses in which two or more factor pairs are heterozygous, no colored-

colorless seeds have been seen except when either *A a* or *C c* is one of the pairs, and here again *A* is more frequently concerned than *C*. Thus, in table 8, where there are listed crosses between various aleurone testers, two anomalous seeds were observed in the nineteen crosses of *A c R* x *A C r*, and two in the ten reciprocal crosses, *A C r* x *A c R* (group 6), in all of which a total of 7170 colored seeds were noted. Of the seven crosses of *a C R* x *A C r* (group 5), involving 2510 colored seeds, two colored-colorless ones were noted, while in the four reciprocal crosses, *A C r* x *a C R*, involving 1160 colored seeds, no seeds of the kind were seen. Again, in seven crosses of *a C R* x *A c R* (group 4), with a total of 2610 colored seeds, there were twenty-six colored-colorless ones, while in five reciprocal crosses, *A c R* x *a C R*, with 1830 colored seeds, there were none not wholly colored. In a single cross of *a C r* x *A C R*, not listed in the table, eight colored-colorless seeds were observed in a total of 450 colored seeds.

In conclusion it can be said that where only a single factor pair is heterozygous and the cross is of such a nature that the contributions of the two parents are known, anomalous seeds have been observed only when the female contributed the recessive and the male the dominant factor. Thus, *a a A* and *c c C* occasionally give rise to colored-colorless seeds, while *A A a* and *C C c* apparently do not. Likewise, when two factor pairs are heterozygous, anomalous colored seeds seem never to be produced except when the female parent contributes one or both of the recessive factors. Similar conditions seem to be essential also for the production of anomalous endosperm where factors other than *A*, *C*, and *R* are concerned. In a previous paper (Emerson, 1915) the writer reported two cases of purple-red seeds and one of a starchy-sugary seed. A third case of a purple-red seed has since been observed. In each of these cases the female parent is known to have contributed the recessive factor and the male parent the dominant factor. Not a single instance of an anomalous seed of any sort is known to the writer in which the male parent is known to have furnished the recessive and the female parent the dominant factor. It seems unlikely that these facts can lack significance.

In the paper just cited (Emerson, 1915), it was pointed out that the vegetative-segregation hypothesis of East and Hayes (1911) could not be applied to the cases there reported if by segregation was meant ordinary Mendelian segregation, in which there are always involved all the

independently inherited Mendelian factors that happen to be heterozygous. The writer therefore suggested the somatic-mutation hypothesis, noted earlier in this paper in connection with the discussion of mottled aleurone. In accordance with this hypothesis, anomalous colored-colorless seeds would not be expected to occur except at extremely infrequent intervals in heterozygotes to which the female parent contributed the dominant factor, and they could hardly be expected ever to occur in homozygotes. If the *A* factor, for instance, might be assumed to mutate with a frequency sufficient to give one colored-colorless seed in every thousand seeds, *A A a* might be expected to exhibit the double mutation to *a a a* once in a million seeds, and *A A A* to undergo the triple mutation to *a a a* once in a billion seeds. Allowing five hundred seeds to an ear, the double mutation might show one anomalous seed in two thousand ears and the triple mutation one in two million ears. On the other hand, in the case of heterozygotes *a a A* one such seed might be expected on the average for every two ears.

The hypothesis of somatic mutations seems to accord well with the facts respecting anomalous aleurone development. Certain other facts, however, make its validity questionable. The *A a* factor pair is concerned in the development of an anthocyanic pigment in the stalk, sheaths, leaves, husks, glumes, anthers, and silks of maize, as well as in the development of aleurone color. In the presence of *A*, a reddish color may develop in any or all of these parts provided they are also exposed to light. If a somatic mutation from *A* to *a* takes place in endosperm development so frequently that, on a heterozygous plant, one seed in a thousand on the average is part colored and part colorless, it seems strange that the same change has never been observed in any other part of the plant. It must be remembered that mutations of the *P* factor resulting in self-colored pericarp in variegated races of maize occur with increasing frequency in the later stages of ontogeny (Emerson, 1917), so that single self-colored seeds are much more frequent than large patches of such seeds and the latter are more frequent than a change affecting a whole ear; but it is also true that plants have been observed to have nearly self-colored ears on one side of a stalk and variegated ears on the other. This mutation is, however, even in the lighter-variegated races, considerably more frequent than is the occurrence of anomalous endosperm. It cannot be said, therefore, that the failure to observe mutations from

*A* to *a* in plant parts other than aleurone disproves the somatic-mutation hypothesis as an explanation of anomalous endosperm development, tho detracting much from such merit as this hypothesis might otherwise have.

It has been suggested by Bartlett[7] that incomplete triple fusion of the nuclei constituting the endosperm nucleus may account for anomalous endosperm development, thus making unnecessary the vegetative-segregation hypothesis of East and Hayes and the somatic-mutation hypothesis of the writer. Bartlett does not outline in detail his ideas regarding the possibilities of incomplete triple fusion, but merely states: "The hypothesis of incomplete triple fusion is in a way a compromise between the inapplicable and discarded older hypotheses involving entire suppression of the triple fusion and the later ones involving no gross cytological aberrations whatever."

If, as previously suggested by the writer (Emerson, 1915), at some early division of the endosperm nucleus of maize, of the constitution *a a A C C C R R R*, the chromosome carrying *A* fails to divide but instead goes bodily to one of the two daughter nuclei, a colored-colorless seed must result. On the contrary, no such result would follow a single such aberrant division if the endosperm nucleus had the constitution *A A a* or *A A A*. In the former of these two cases, two, and in the latter case three, such aberrant divisions would have to occur in the development of the same seed to result in any group of cells of the nature of *a a a*. The same would, of course, be true for *C*, *R*, *Pr*, or the factor for starchy endosperm, *Su*. Tho the writer is not aware of any cytological evidence of such aberrant behavior in divisions of the endosperm nuclei of maize, if found they would account for the facts regarding aleurone color development reported in this paper quite as well as the hypothesis of somatic mutation, and would at the same time explain why no change from red to non-red color in other plant parts depending on the *A a* factor pair is observed. If some other endosperm factor pair linked with *A a* could be found, definite evidence rendering untenable one or the other of the two hypotheses might be obtained. While no endosperm factor is known to be linked with *A*, waxy endosperm is thus associated with *C* (Bregger, 1918). The percentage of crossing-over between *C* and the factor for

[7] Bartlett, H. H. Anomalous endosperm and the problem of bud sports Bot. gaz. 62:247-248 1916.

waxy endosperm, *wx*, is from about 22 to 27. The supposition is, therefore, on the chromosome theory of heredity, that *C* and *Wx* lie in the same chromosome and about 22 to 27 units apart. A mutation affecting *C* would consequently not be expected necessarily to affect *Wx*. If, on the other hand, the chromosome carrying *C* failed to divide, so that one of the resulting daughter nuclei lacked *C*, *Wx* must also go to the same daughter nucleus receiving *C*. If, then, the endosperm were heterozygous for *C* and *Wx* only, and of the constitution *c c C wx wx Wx*, the colored part of the seed must be starchy and the colorless part waxy. Collins (1912) reported an anomalous seed, one part of which was colorless starchy and the remainder colored waxy, from a cross of a colored waxy plant pollinated by a colorless starchy one. It is not known, however, what aleurone factor or factors may have been involved. A solution of this problem must therefore await further investigation.

## SUMMARY

In addition to the four factor pairs concerned in the development of aleurone color in maize, *C c*, *R r*, *I i*, and *Pr pr*, a fifth pair, *A a*, is announced. The interrelations of these factors are such that dominant *A*, *C*, and *R*, and duplex recessive *i*, must all be present in order that any aleurone color may develop. Duplex *pr*, together with the other factors, results in red aleurone, while *Pr* similarly gives purple.

Instances are reported of $F_2$ ratios of colored to colorless approaching 27:37. These are compared with the well-known 9:7 $F_2$ ratios. The variation in percentage of colorless individuals is sufficient to cause an overlapping of the two classes, the range for the 9:7 class being from 36 to 53.7 per cent and for the 27:37 class from 44.9 to 66.5 per cent. The mean $F_2$ percentages were found to be $42.91 \pm 0.28$ for the 9:7 class and $57.79 \pm 0.21$ for the 27:37 class, while the theoretical percentages are 43.75 and 57.81, respectively.

The hypothesis proposed to account for 27:37 ratios — namely, that color develops only in the presence of the three dominant factors *A*, *C*, and *R* and that all three were heterozygous in $F_1$ — has been subjected to every genetic test known to the writer, with results quite in accord with expectation, as follows: (1) Colorless $F_2$ individuals have bred true colorless in $F_3$. Colored $F_2$ individuals are shown to be of four kinds

with respect to their behavior in $F_3$, giving ratios of colored to colorless of 1:0, 3:1, 9:7, and 27:37 in approximately the expected numerical relation of 1:6:12:8, respectively. For comparison, colored $F_2$ individuals of the 9:7 class were tested, and these were found to give $F_3$ ratios of 1:0, 3:1, and 9:7 in about the expected numerical relation of 1:4:4, respectively. The results in $F_4$, so far as determined, were in agreement with the hypothesis. (2) The seven classes of colorless individuals expected on the basis of the hypothesis, namely, *a C R*, *A c R*, *A C r*, *A c r*, *a C r*, *a c R*, and *a c r*, have been found. Demonstration of the existence of these several classes has been made possible by use in crosses of the three classes, *a C R*, *A c R*, and *A C r*, known as aleurone testers, after these had first been isolated by random intercrosses of colorless individuals.

Results to be expected from crossing the three aleurone testers with each of the twenty-seven possible genotypes involving *A*, *C*, and *R* are shown, and examples illustrating some of these results are given.

The effect of degree of maturity on the development of aleurone color is pointed out, and the difference in appearance of aleurone colors due to the color, composition, and texture of the underlying endosperm is discussed.

Certain previously unannounced genetic factors influencing aleurone color and color patterns are noted. The mode of inheritance of some of these, and their interrelations with other aleurone factors, have not as yet been fully determined.

Heterozygous mottling of aleurone color is shown to be due to the *R r* factor pair or to some factor closely associated with it. It is shown by means of reciprocal crosses that mottling occurs only when *R* is contributed by the male parent and *r* by the female parent of a cross, thus indicating that colored aleurone of the constitution *R R R* or *R R r* is self-colored while that of the constitution *r r R* is ordinarily mottled. Various hypotheses bearing upon the relation of *R* to mottling are discussed.

Examples are given of anomalous development of aleurone color resulting in seeds that are partly colored and partly colorless. It is shown that *R* is rarely if ever concerned in this peculiar coloration, while *C* and *A*, the latter probably more frequently than the former, are so concerned.

Such colored-colorless seeds apparently occur only when at least one of the aleurone color factors is heterozygous, and then only when the dominant factor enters the cross from the male parent and its recessive allelomorph from the female parent. From these facts it is inferred that the *a a A* condition of the aleurone, for instance, but not the *A A a* and *A A A* conditions, may occasionally result in anomalously colored seeds. Three possibilities are discussed in this connection — vegetative segregation, somatic mutation, and aberrant chromosome behavior.

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## TABLES

TABLE 1. RECORDS OF ALEURONE COLOR IN SIXTY-ONE $F_2$ PROGENIES OF CROSSES OF COLORLESS x COLORLESS AND COLORED x COLORLESS PARENTS

(Fig. 71, B)

| Pedigree no. | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev./P. E. |
|---|---|---|---|---|---|---|
| | Colored | Colorless | Total | | | |
| 1545– 3 | 213 | 348 | 561 | 62.0±1.4 | + 4.2 | 3.0 |
| 4 | 57 | 59 | 116 | 50.9±3.1 | — 6.9 | 2.2 |
| 11 | 239 | 306 | 545 | 56.1±1.4 | — 1.7 | 1.2 |
| 14 | 254 | 374 | 628 | 59.6±1.3 | + 1.8 | 1.4 |
| 16 | 244 | 300 | 544 | 55.1±1.4 | — 2.7 | 1.9 |
| 1981–20 | 38 | 31 | 69 | 44.9±4.0 | —12.9 | 3.2 |
| 1982– 2 | 54 | 93 | 147 | 63.3±2.7 | + 5.5 | 2.0 |
| 3 | 236 | 338 | 574 | 58.9±1.4 | + 1.1 | 0.8 |
| 10 | 171 | 186 | 357 | 52.1±1.8 | — 5.7 | 3.2 |
| 13 | 290 | 418 | 708 | 59.0±1.3 | + 1.2 | 0.9 |
| 14 | 87 | 129 | 216 | 59.7±2.3 | + 1.9 | 0.8 |
| 1987–17 | 46 | 76 | 122 | 62.3±3.0 | + 4.5 | 1.5 |
| 1989–10 | 196 | 289 | 485 | 59.6±1.5 | + 1.8 | 1.2 |
| 17 | 15 | 21 | 36 | 58.3±5.6 | + 0.5 | 0.1 |
| 18 | 51 | 74 | 125 | 59.2±3.0 | + 1.4 | 0.5 |
| 2407– 1 | 84 | 77 | 161 | 47.8±2.6 | —10.0 | 3.8 |
| 2 | 48 | 68 | 116 | 58.6±3.1 | + 0.8 | 0.3 |
| 2894– 1 | 231 | 305 | 536 | 56.9±1.4 | — 0.9 | 0.6 |
| 2 | 143 | 143 | 286 | 50.0±2.0 | — 7.8 | 3.9 |
| 3 | 111 | 145 | 256 | 56.6±2.1 | — 1.2 | 0.6 |
| 4 | 303 | 402 | 705 | 57.0±1.3 | — 0.8 | 0.6 |
| 5 | 270 | 375 | 645 | 58.1±1.3 | + 0.3 | 0.2 |
| 5289– 1 | 200 | 301 | 501 | 60.1±1.5 | + 2.3 | 1.5 |
| 6 | 224 | 262 | 486 | 53.9±1.5 | — 3.9 | 2.6 |
| 5313– 1 | 176 | 246 | 422 | 58.3±1.6 | + 0.5 | 0.3 |
| 4 | 200 | 268 | 468 | 57.3±1.5 | — 0.5 | 0.3 |
| 5 | 40 | 66 | 106 | 62.3±3.2 | + 4.5 | 1.4 |
| 7 | 174 | 208 | 382 | 54.5±1.7 | — 3.3 | 1.9 |
| 9 | 195 | 326 | 521 | 62.6±1.5 | + 4.8 | 3.2 |
| 7032– 1 | 124 | 192 | 316 | 60.8±1.9 | + 3.0 | 1.6 |
| 7033– 9 | 154 | 306 | 460 | 66.5±1.6 | + 8.7 | 5.4 |
| 7034– 5 | 82 | 87 | 169 | 51.5±2.6 | — 6.3 | 2.4 |
| 7036– 3 | 56 | 96 | 152 | 63.2±2.7 | + 5.4 | 2.0 |
| 7037– 2 | 45 | 86 | 131 | 65.6±2.9 | + 7.8 | 2.7 |
| 4 | 73 | 73 | 146 | 50.0±2.8 | — 7.8 | 2.8 |
| L829– 3 | 240 | 344 | 584 | 58.9±1.4 | + 1.1 | 0.8 |
| 7 | 135 | 210 | 345 | 60.9±1.8 | + 3.1 | 1.7 |
| 8 | 231 | 323 | 554 | 58.3±1.4 | + 0.5 | 0.4 |
| 9 | 191 | 278 | 469 | 59.3±1.5 | + 1.5 | 1.0 |
| 10 | 184 | 243 | 427 | 56.9±1.6 | — 0.9 | 0.6 |
| 12 | 202 | 244 | 446 | 54.7±1.6 | — 3.1 | 1.9 |

TABLE 1 (*concluded*)

| Pedigree no. | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev./P. E. |
|---|---|---|---|---|---|---|
| | Colored | Colorless | Total | | | |
| L882- 1 | 238 | 274 | 512 | 53.5±1.5 | — 4.3 | 2.9 |
| 2 | 242 | 381 | 623 | 61.2±1.3 | + 3.4 | 2.6 |
| 3 | 153 | 202 | 355 | 56.9±1.8 | — 0.9 | 0.5 |
| 5 | 196 | 284 | 480 | 59.2±1.5 | + 1.4 | 0.9 |
| 7 | 192 | 283 | 475 | 59.6±1.5 | + 1.8 | 1.2 |
| 8 | 224 | 258 | 482 | 53.5±1.5 | — 4.3 | 2.9 |
| 9 | 272 | 347 | 619 | 56.1±1.3 | — 1.7 | 1.3 |
| 10 | 168 | 263 | 431 | 61.0±1.6 | + 3.2 | 2.0 |
| 11 | 248 | 339 | 587 | 57.8±1.4 | 0 | 0 |
| 12 | 221 | 281 | 502 | 56.0±1.5 | — 1.8 | 1.2 |
| 13 | 231 | 271 | 502 | 54.0±1.5 | — 3.8 | 2.5 |
| 14 | 194 | 224 | 418 | 53.6±1.6 | — 4.2 | 2.6 |
| 15 | 246 | 356 | 602 | 59.1±1.4 | + 1.3 | 0.9 |
| 16 | 262 | 373 | 635 | 58.7±1.3 | + 0.9 | 0.7 |
| 17 | 296 | 387 | 683 | 56.7±1.3 | — 1.1 | 0.8 |
| 18 | 186 | 301 | 487 | 61.8±1.5 | + 4.0 | 2.7 |
| 19 | 190 | 237 | 427 | 55.5±1.6 | — 2.3 | 1.4 |
| 20 | 185 | 266 | 451 | 59.0±1.6 | + 1.2 | 0.7 |
| 21 | 186 | 244 | 430 | 56.7±1.6 | — 1.1 | 0.7 |
| 22 | 237 | 328 | 565 | 58.1±1.4 | + 0.3 | 0.2 |
| Total | 10,674 | 14,615 | 25,289 | 57.8±0.2 | 0 | 0 |

* Probable errors are determined from the formula $0.6744898\sqrt{\frac{pq}{n}}$, in which $n$ is the number of individuals and $p$ and $q$ are the percentages corresponding to the 27:37 ratio, namely, 42.1875 and 57.8125. Values of $\frac{0.6744898}{\sqrt{n}}$ are taken from Gibson's tables (Biometrika 4:385–393. 1905–06).

† Deviations are calculated from 57.8 per cent.

TABLE 2. RECORDS OF ALEURONE COLOR IN FIFTY-ONE $F_2$ PROGENIES OF CROSSES OF COLORED x COLORLESS PARENTS

(Fig. 71, A)

| Pedigree no. | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P. E. |
|---|---|---|---|---|---|---|
| | Colored | Colorless | Total | | | |
| 1212- 1 | 189 | 146 | 335 | 43.6±1.8 | —0.2 | 0.1 |
| 4 | 262 | 190 | 452 | 42.0±1.6 | —1.8 | 1.1 |
| 32 | 99 | 77 | 176 | 43.8±2.5 | 0 | 0 |
| 37 | 258 | 179 | 437 | 41.0±1.6 | —2.8 | 1.7 |
| 42 | 188 | 123 | 311 | 39.5±1.9 | —4.3 | 2.3 |
| 1878- 7 | 211 | 157 | 368 | 42.7±1.7 | —1.1 | 0.6 |
| 8 | 45 | 50 | 95 | 52.6±3.4 | +8.8 | 2.6 |
| 12 | 146 | 115 | 261 | 44.1±2.1 | +0.3 | 0.1 |
| 17 | 31 | 20 | 51 | 39.2±4.7 | —4.6 | 1.0 |
| 20 | 138 | 101 | 239 | 42.3±2.2 | —1.5 | 0.7 |
| 1882- 2 | 143 | 106 | 249 | 42.6±2.1 | —1.2 | 0.6 |
| 3 | 70 | 59 | 129 | 45.7±2.9 | +1.9 | 0.7 |
| 12 | 125 | 84 | 209 | 40.2±2.3 | —3.6 | 1.6 |
| 14 | 142 | 120 | 262 | 45.8±2.1 | +2.0 | 1.0 |
| 17 | 36 | 33 | 69 | 47.8±4.0 | +4.0 | 1.0 |
| 1986- 6 | 95 | 62 | 157 | 39.5±2.7 | —4.3 | 1.6 |
| 1987- 2 | 259 | 195 | 454 | 43.0±1.6 | —0.8 | 0.5 |
| 1989- 7 | 34 | 26 | 60 | 43.3±4.3 | —0.5 | 0.1 |
| 9 | 205 | 175 | 380 | 46.1±1.7 | +2.3 | 1.4 |
| 12 | 136 | 101 | 237 | 42.6±2.2 | —1.2 | 0.5 |
| 14 | 54 | 46 | 100 | 46.0±3.3 | +2.2 | 0.7 |
| 16 | 170 | 120 | 290 | 41.4±2.0 | —2.4 | 1.2 |
| 2520- 1 | 32 | 18 | 50 | 36.0±4.7 | —7.8 | 1.7 |
| 2 | 32 | 27 | 59 | 45.8±4.4 | +2.0 | 0.5 |
| 3 | 57 | 46 | 103 | 44.7±3.3 | +0.9 | 0.3 |
| 2848- 1 | 358 | 264 | 622 | 42.4±1.3 | —1.4 | 1.1 |
| 2 | 180 | 159 | 339 | 46.9±1.8 | +3.1 | 1.7 |
| 3 | 236 | 152 | 388 | 39.2±1.7 | —5.4 | 3.2 |
| 4 | 249 | 173 | 422 | 41.0±1.6 | —2.8 | 1.7 |
| 5 | 155 | 130 | 285 | 45.6±2.0 | +1.8 | 0.9 |
| 6 | 238 | 176 | 414 | 42.5±1.6 | —1.3 | 0.8 |
| 8 | 272 | 231 | 503 | 45.9±1.5 | +2.1 | 1.4 |
| 2877- 1 | 277 | 233 | 510 | 45.7±1.5 | +1.9 | 1.3 |
| 3 | 27 | 21 | 48 | 43.7±4.8 | —0.1 | 0 |
| 4 | 23 | 15 | 38 | 39.5±5.4 | —4.3 | 0.8 |
| 6 | 25 | 29 | 54 | 53.7±4.6 | +9.9 | 2.2 |
| 7 | 135 | 104 | 239 | 43.5±2.2 | —0.3 | 0.1 |
| 9 | 298 | 214 | 512 | 41.8±1.5 | —2.0 | 1.3 |
| 10 | 121 | 98 | 219 | 44.7±2.3 | +0.9 | 0.4 |
| 2878- 7 | 229 | 168 | 397 | 42.3±1.7 | —1.5 | 0.9 |
| 4259- 1 | 103 | 65 | 168 | 38.7±2.6 | —5.1 | 2.0 |
| 2 | 172 | 110 | 282 | 39.0±2.0 | —4.8 | 2.4 |

* Probable errors are based on the assumption of 9:7 ratios, with $p$ and $q$ taken, therefore, as 56.25 and 43.75 per cent, respectively.

† Deviations are calculated from 43.8 per cent.

TABLE 2 (*concluded*)

| Pedigree no. | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev./P. E. |
|---|---|---|---|---|---|---|
| | Colored | Colorless | Total | | | |
| 4259– 3 | 316 | 205 | 521 | 39.3±1.5 | —4.5 | 3.0 |
| 4 | 288 | 240 | 528 | 45.5±1.5 | +1.7 | 1.1 |
| 6 | 293 | 180 | 473 | 38.1±1.5 | —5.7 | 3.8 |
| 7 | 189 | 153 | 342 | 44.7±1.8 | +0.9 | 0.5 |
| 8 | 283 | 204 | 487 | 41.9±1.5 | —1.9 | 1.3 |
| 9 | 238 | 176 | 414 | 42.5±1.6 | —1.3 | 0.8 |
| 10 | 285 | 225 | 510 | 44.1±1.5 | +0.3 | 0.2 |
| 4452– 2 | 176 | 148 | 324 | 45.7±1.9 | +1.9 | 1.0 |
| 3 | 79 | 63 | 142 | 44.4±2.8 | +0.6 | 0.2 |
| Total | 8,402 | 6,312 | 14,714 | 42.9±0.3 | —0.9 | 3.0 |

* Probable errors are based on the assumption of 9:7 ratios, with $p$ and $q$ taken, therefore, as 56.25 and 43.75 per cent, respectively.
† Deviations are calculated from 43.8 per cent.

TABLE 3. RECORDS OF ALEURONE COLOR IN FORTY $F_3$ AND $F_4$ PROGENIES OF COLORLESS $F_2$ AND $F_3$ INDIVIDUALS, RESPECTIVELY, FROM GROUPS B AND D–G OF FIGURE 71

| Ratios of preceding generation | Group | Pedigree no. | | Number of individuals | |
|---|---|---|---|---|---|
| | | $F_2$ | $F_3$ | Colored | Colorless* |
| 27:37 | 1 | 1545–16 | 1985–48 | 0 | 480 |
| | | 1981–20 | 2853– 2 | 0 | 20 |
| | | | 5 | 0 | 640 |
| | | | 6 | 0 | 250 |
| | | | 11 | 0 | 40 |
| | | | 12 | 0 | 20 |
| | | | 14 | 0 | 450 |
| | | | 15 | 1 | 430 |
| | | | 18 | 0 | 420 |
| | | 2407– 1 | 2890– 1 | 0 | 480 |
| | | | 3 | 0 | 240 |
| | | | 4 | 1 | 540 |
| | | | 5 | 0 | 720 |
| | | | 2891– 1 | 1 | 770 |
| | | | 5 | 0 | 430 |
| | | Total, 15 progenies | | 3 | 5,930 |

* The numbers were recorded to the ten nearest the product of the number of rows of seeds and the number of seeds in one row.

TABLE 3 (*concluded*)

| Ratios of preceding generation | Group | Pedigree no. | | Number of individuals | |
|---|---|---|---|---|---|
| | | $F_3$ | $F_4$ | Colored | Colorless* |
| 3:1 | 2 | 1893–44 | 2871– 1 | 0 | 170 |
| | | 9 | 2873– 3 | 0 | 380 |
| | | 74 | 2875– 1 | 0 | 470 |
| | | | 4 | 0 | 400 |
| | | | 5 | 0 | 480 |
| | | | 9 | 0 | 110 |
| | | Total, 6 progenies | | 0 | 2,010 |
| 9:7 | 3 | 1983– 3 | 2865– 1 | 0 | 160 |
| | | | 5 | 0 | 70 |
| | | 1983–87 | 2868– 4 | 0 | 180 |
| | | | 7 | 0 | 60 |
| | | Total, 4 progenies | | 0 | 470 |
| 27:37 | 4 | 1983–36 | 2856– 3 | 0 | 480 |
| | | | 4 | 0 | 180 |
| | | | 5 | 0 | 380 |
| | | | 2857– 1 | 0 | 420 |
| | | | 2 | 0 | 370 |
| | | | 4 | 0 | 190 |
| | | | 2858– 1 | 0 | 200 |
| | | | 3 | 0 | 110 |
| | | | 4 | 0 | 180 |
| | | | 5 | 1 | 220 |
| | | | 6 | 0 | 150 |
| | | 1983–23 | 2862– 1 | 0 | 120 |
| | | | 2 | 0 | 140 |
| | | | 5 | 0 | 80 |
| | | | 8 | 0 | 30 |
| | | Total, 15 progenies | | 1 | 3,250 |

* The numbers were recorded to the ten nearest the product of the number of rows of seeds and the number of seeds in one row.

TABLE 4. RECORDS OF ALEURONE COLOR IN EIGHTY-EIGHT $F_3$ PROGENIES OF COLORED $F_2$ INDIVIDUALS OF TABLE 1 AND GROUP B, FIGURE 71

(Fig. 71, C–G)

| Group | Pedigree no. | | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | Colored | Colorless | Total | | | |
| C | 1545–16 | 1983–59 | 13 | 0 | 13 | 0 | ..... | ..... |
| | | 1984–20 | 150 | 0 | 150 | 0 | ..... | ..... |
| | 5289– 1 | 7132–31 | 392 | 0 | 392 | 0 | ..... | ..... |
| | Total, 3 progenies | | 555 | 0 | 555 | 0 | ..... | ..... |
| D | 1545–16 | 1983– 9 | 49 | 15 | 64 | 23.4±3.7 | —1.6 | 0.4 |
| | | 34 | 28 | 11 | 39 | 28.2±4.7 | +3.2 | 0.7 |
| | | 40 | 329 | 101 | 430 | 23.5±1.4 | —1.5 | 1.1 |
| | | 43 | 155 | 53 | 208 | 25.5±2.0 | +0.5 | 0.2 |
| | | 44 | 44 | 13 | 57 | 22.8±3.9 | —2.2 | 0.6 |
| | | 50 | 165 | 46 | 211 | 21.8±2.0 | —3.2 | 1.6 |
| | | 74 | 87 | 27 | 114 | 23.7±2.7 | —1.3 | 0.5 |
| | | 85 | 186 | 74 | 260 | 28.5±1.8 | +3.5 | 1.9 |
| | | 101 | 79 | 25 | 104 | 24.0±2.9 | —1.0 | 0.3 |
| | | 1984– 5 | 24 | 6 | 30 | 20.0±5.3 | —5.0 | 0.9 |
| | | 9 | 306 | 94 | 400 | 23.5±1.5 | —1.5 | 1.0 |
| | 1981–20 | 2854– 1 | 185 | 68 | 253 | 26.9±1.8 | +1.9 | 1.1 |
| | | 7 | 343 | 101 | 444 | 22.7±1.4 | —2.3 | 1.6 |
| | | 2855– 3 | 38 | 14 | 52 | 26.9±4.0 | +1.9 | 0.5 |
| | 5289– 1 | 7132–35 | 146 | 46 | 192 | 24.0±2.1 | —1.0 | 0.5 |
| | | 61 | 158 | 52 | 210 | 24.8±2.0 | —0.2 | 0.1 |
| | | 67 | 172 | 59 | 231 | 25.5±1.9 | +0.5 | 0.3 |
| | | 84 | 71 | 26 | 97 | 26.8±3.0 | +1.8 | 0.6 |
| | Total, 18 progenies | | 2,565 | 831 | 3,396 | 24.5±0.5 | —0.5 | 1.0 |
| F | 1545–16 | 1983– 3 | 261 | 235 | 496 | 47.4±1.5 | +3.6 | 2.4 |
| | | 36 | 178 | 172 | 350 | 49.1±1.8 | +5.3 | 2.9 |
| | | 45 | 77 | 71 | 148 | 48.0±2.8 | +4.2 | 1.5 |
| | | 46 | 258 | 194 | 452 | 42.9±1.6 | —0.9 | 0.6 |
| | | 66 | 64 | 61 | 125 | 48.8±3.0 | +5.0 | 1.7 |
| | | 70 | 31 | 23 | 54 | 42.6±4.6 | —1.2 | 0.3 |
| | | 76 | 219 | 158 | 377 | 41.9±1.7 | —1.9 | 1.1 |
| | | 95 | 20 | 15 | 35 | 42.9±5.7 | —0.9 | 0.2 |
| | | 96 | 56 | 39 | 95 | 41.1±3.4 | —2.7 | 0.8 |
| | | 100 | 16 | 10 | 26 | 38.4±6.6 | —5.4 | 0.8 |
| | | 1984– 3 | 105 | 101 | 206 | 49.3±2.3 | +5 5 | 2.4 |
| | | 11 | 10 | 10 | 20 | 50.0±7.5 | +6.2 | 0.8 |

* Probable errors are calculated on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for group D, 56.25 and 43.75 per cent for group F, and 42.1875 and 57.8125 per cent for group G.

† Deviations are calculated from 25 per cent in group D, from 43.8 per cent in group F, and from 57.8 per cent in group G.

TABLE 4 (*continued*)

| Group | Pedigree no. | | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | Colored | Colorless | Total | | | |
| F (*concluded*) | 1545-16 | 1984-19 | 10 | 7 | 17 | 41.2±8.1 | —2.6 | 0.3 |
| | | 28 | 132 | 90 | 222 | 40.5±2.2 | —3.3 | 1.5 |
| | 1981-20 | 2854- 5 | 92 | 59 | 152 | 39.1±2.7 | —4.7 | 1.7 |
| | | 10 | 210 | 149 | 359 | 41.5±1.8 | —2.3 | 1.3 |
| | | 11 | 34 | 28 | 62 | 45.2±4.2 | +1.4 | 0.3 |
| | | 15 | 223 | 176 | 399 | 44.1±1.7 | +0.3 | 0.2 |
| | | 2855- 8 | 59 | 46 | 105 | 43.8±3.3 | 0 | 0 |
| | 1982- 2 | 4478- 2 | 79 | 63 | 142 | 44.4±2.8 | +0.6 | 0.2 |
| | 2407- 1 | 2892- 6 | 120 | 95 | 215 | 44.2±2.3 | +0.4 | 0.2 |
| | 5289- 1 | 7132- 1 | 175 | 154 | 329 | 46.8±1.8 | +3.0 | 1.7 |
| | | 4 | 281 | 201 | 482 | 41.7±1.5 | —2.1 | 1.4 |
| | | 5 | 173 | 142 | 315 | 45.1±1.9 | +1.3 | 0.7 |
| | | 9 | 99 | 81 | 180 | 45.0±2.5 | +1.2 | 0.5 |
| | | 12 | 161 | 132 | 293 | 45.1±2.0 | +1.3 | 0.6 |
| | | 19 | 143 | 112 | 255 | 43.9±2.1 | +0.1 | 0 |
| | | 47 | 141 | 127 | 268 | 47.4±2.0 | +3.6 | 1.8 |
| | | 50 | 178 | 148 | 326 | 45.4±1.9 | +1.6 | 0.8 |
| | | 57 | 187 | 107 | 294 | 36.4±2.0 | —7.4 | 3.7 |
| | | 59 | 227 | 173 | 400 | 43.2±1.7 | —0.6 | 0.4 |
| | Total, 31 progenies | | 4,019 | 3,179 | 7,198 | 44.2±0.4 | +0.4 | 1.0 |
| G | 1545-16 | 1983- 4 | 55 | 93 | 148 | 62.8±2.7 | +5.0 | 1.9 |
| | | 23 | 174 | 208 | 382 | 54.5±1.7 | —3.3 | 1.9 |
| | | 31 | 42 | 54 | 96 | 56.2±3.4 | —1.6 | 0.5 |
| | | 49 | 55 | 84 | 139 | 60.4±2.8 | +2.6 | 0.9 |
| | | 63 | 28 | 29 | 57 | 50.9±4.4 | —6.9 | 1.6 |
| | | 71 | 15 | 16 | 31 | 51.6±6.0 | —6.2 | 1.0 |
| | | 73 | 114 | 134 | 248 | 54.0±2.1 | —3.8 | 1.8 |
| | | 86 | 13 | 23 | 36 | 63.9±5.6 | +6.1 | 1.1 |
| | | 87 | 60 | 63 | 123 | 51.2±3.0 | —6.6 | 2.2 |
| | | 89 | 28 | 29 | 57 | 50.9±4.4 | —6.9 | 1.6 |
| | | 97 | 85 | 104 | 189 | 55.0±2.4 | —2.8 | 1.2 |
| | | 98 | 153 | 214 | 367 | 58.3±1.7 | +0.5 | 0.3 |
| | | 1984- 8 | 90 | 112 | 202 | 55.4±2.3 | —2.4 | 1.0 |
| | | 12 | 31 | 34 | 65 | 52.3±4.1 | —5.5 | 1.3 |
| | | 14 | 23 | 35 | 58 | 60.3±4.4 | +2.5 | 0.6 |
| | | 16 | 127 | 156 | 283 | 55.1±2.0 | —2.7 | 1.3 |
| | | 22 | 76 | 96 | 172 | 55.8±2.5 | —2.0 | 0.8 |
| | | 23 | 25 | 26 | 51 | 51.0±4.7 | —6.8 | 1.4 |
| | 1981-20 | 2854- 3 | 197 | 259 | 456 | 56.8±1.6 | —1.0 | 0.6 |

* Probable errors are calculated on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for group D, 56.25 and 43.75 per cent for group F, and 42.1875 and 57.8125 per cent for group G.

† Deviations are calculated from 25 per cent in group D, from 43.8 per cent in group F, and from 57.8 per cent in group G.

TABLE 4 (*concluded*)

| Group | Pedigree no. | | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P E. |
|---|---|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | Colored | Colorless | Total | | | |
| G (*concluded*) | 1981–20 | 16 | 117 | 187 | 304 | 61.5±1.9 | +3.7 | 1.9 |
| | | 2855– 5 | 17 | 34 | 51 | 66.7±4.7 | +8.9 | 1.9 |
| | | 6 | 240 | 308 | 548 | 56.2±1.4 | —1.6 | 1.1 |
| | | 7 | 22 | 29 | 51 | 56.9±4.7 | —0.9 | 0.2 |
| | 1982– 2 | 4478– 3 | 78 | 105 | 183 | 57.4±2.5 | —0.4 | 0.2 |
| | 2407– 1 | 2892– 2 | 107 | 137 | 244 | 56.1±2.1 | —1.7 | 0.8 |
| | | 7 | 160 | 228 | 388 | 58.8±1.7 | +1.0 | 0.6 |
| | 5289– 1 | 7132–16 | 117 | 146 | 263 | 55.5±2.1 | —2.3 | 1.1 |
| | | 22 | 50 | 59 | 109 | 54.1±3.2 | —3.7 | 1.2 |
| | | 27 | 48 | 86 | 134 | 64.2±2.9 | +6.4 | 2.2 |
| | | 36 | 103 | 123 | 226 | 54.4±2.2 | —3.4 | 1.5 |
| | | 38 | 144 | 203 | 347 | 58.5±1.8 | +0.7 | 0.4 |
| | | 55 | 150 | 224 | 374 | 59.9±1.7 | +2.1 | 1.2 |
| | | 60 | 156 | 197 | 353 | 55.8±1.8 | —2.0 | 1.1 |
| | | 62 | 136 | 180 | 316 | 57.0±1.9 | —0.8 | 0.4 |
| | | 66 | 132 | 189 | 321 | 58.9±1.9 | +1.1 | 0.6 |
| | | 76 | 142 | 201 | 343 | 58.6±1.8 | +0.8 | 0.4 |
| | Total, 36 progenies | | 3,310 | 4,405 | 7,715 | 57.1±0.4 | —0.7 | 1.7 |

*Probable errors are calculated on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for group D, 56.25 and 43.75 per cent for group F, and 42.1875 and 57.8125 per cent for group G.

† Deviations are calculated from 25 per cent in group D, from 43.8 per cent in group F, and from 57.8 per cent in group G.

TABLE 5. RECORDS OF ALEURONE COLOR IN FIFTY-FOUR $F_3$ AND $F_4$ PROGENIES OF COLORED $F_2$ AND $F_3$ INDIVIDUALS, RESPECTIVELY, OF TABLE 2 AND GROUP A, FIGURE 71 (Fig. 71, H–J)

| Group | Pedigree no. | | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|
| | | | Colored | Colorless | Total | | | |
| | $F_2$ | $F_3$ | | | | | | |
| | 1212–32 | 1880– 4 | 168 | 0 | 168 | 0 | ..... | ..... |
| | | 9 | 214 | 0 | 214 | 0 | ..... | ..... |
| | | 21 | 242 | 0 | 242 | 0 | ..... | ..... |
| | 37 | 1962–41 | 200 | 0 | 200 | 0 | ..... | ..... |
| H | 42 | 1886–13 | 71 | 0 | 71 | 0 | ..... | ..... |
| | | 15 | 205 | 0 | 205 | 0 | ..... | ..... |
| | $F_3$ | $F_4$ | | | | | | |
| | 1876–17 | 1973–16 | 121 | 0 | 121 | 0 | ..... | ..... |
| | Total, 7 progenies | | 1,221 | 0 | 1,221 | 0 | ..... | ..... |
| | $F_2$ | $F_3$ | | | | | | |
| | 1212–32 | 1880–10 | 232 | 70 | 302 | 23.2±1.7 | —1.8 | 1.1 |
| | | 12 | 194 | 56 | 250 | 22.4±1.8 | —2.6 | 1.4 |
| | | 18 | 75 | 30 | 105 | 28.6±2.9 | +3.6 | 1.2 |
| | 37 | 1876– 4 | 42 | 12 | 54 | 22.2±4.0 | —2.8 | 0.7 |
| | | 11 | 192 | 76 | 268 | 28.4±1.8 | +3.4 | 1.9 |
| | | 18 | 92 | 31 | 123 | 25.2±2.6 | +0.2 | 0.1 |
| | | 19 | 263 | 96 | 359 | 26.7±1.5 | +1.7 | 1.1 |
| | | 1962– 2 | 168 | 51 | 219 | 23.3±2.0 | —1.7 | 0.8 |
| | | 3 | 15 | 6 | 21 | 28.6±6.4 | +3.6 | 0.6 |
| | | 8 | 178 | 67 | 245 | 27.3±1.9 | +2.3 | 1.2 |
| | | 9 | 112 | 38 | 150 | 25.3±2.4 | +0.3 | 0.1 |
| | | 10 | 63 | 27 | 90 | 30.0±3.1 | +5.0 | 1.6 |
| I | | 14 | 70 | 23 | 93 | 24.7±3.0 | —0.3 | 0.1 |
| | | 20 | 245 | 77 | 322 | 23.9±1.6 | —1.1 | 0.7 |
| | | 22 | 99 | 31 | 130 | 23.8±2.6 | —1.2 | 0.5 |
| | | 36 | 155 | 49 | 204 | 24.0±2.0 | —1.0 | 0.5 |
| | | 38 | 130 | 46 | 176 | 26.1±2.2 | +1.1 | 0.5 |
| | 42 | 1886– 3 | 57 | 18 | 75 | 24.0±3.4 | —1.0 | 0.3 |
| | $F_3$ | $F_4$ | | | | | | |
| | 1876–17 | 1973– 2 | 116 | 39 | 155 | 25.2±2.3 | +0.2 | 0.1 |
| | | 5 | 146 | 47 | 193 | 24.4±2.1 | —0.6 | 0.3 |
| | | 6 | 92 | 34 | 126 | 26.9±2.6 | +1.9 | 0.7 |
| | 1962–21 | 2846– 1 | 160 | 42 | 202 | 20.8±2.1 | —4.2 | 2.0 |
| | | 10 | 198 | 68 | 266 | 25.6±1.8 | +0.6 | 0.3 |
| | Total, 23 progenies | | 3,094 | 1,034 | 4,128 | 25.0±0.5 | 0 | 0 |

* Probable errors are based on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for group I, and 56.25 and 43.75 per cent for group J.

† Deviations are calculated from 25 per cent in group I and 43.8 per cent in group J.

TABLE 5 (*concluded*)

| Group | Pedigree no. | | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|
| | | | Colored | Color-less | Total | | | |
| | $F_2$ | $F_3$ | | | | | | |
| | 1212– 1 | 1884– 1 | 63 | 46 | 109 | 42.2±3.2 | —1.6 | 0.5 |
| | | 2 | 111 | 80 | 191 | 41.9±2.4 | —1.9 | 0.8 |
| | | 5 | 45 | 37 | 82 | 45.1±3.7 | +1.3 | 0.4 |
| | 4 | 1890– 1 | 10 | 7 | 17 | 41.2±8.1 | —2.6 | 0.3 |
| | | 2 | 146 | 95 | 241 | 39.4±2.2 | —4.4 | 2.0 |
| | | 8 | 127 | 100 | 227 | 44.1±2.2 | +0.3 | 0.1 |
| | 32 | 1880– 1 | 176 | 116 | 292 | 39.7±2.0 | —4.1 | 2.0 |
| | | 8 | 73 | 66 | 139 | 47.5±2.8 | +3.7 | 1.3 |
| | | 15 | 65 | 48 | 113 | 42.5±3.1 | —1.3 | 0.4 |
| | | 20 | 98 | 67 | 165 | 40.6±2.6 | —3.2 | 1.2 |
| | 37 | 1876–17 | 58 | 44 | 102 | 43.1±3.3 | —0.7 | 0.2 |
| | | 1962–21 | 124 | 100 | 224 | 44.6±2.2 | +0.8 | 0.4 |
| J | | 45 | 55 | 39 | 94 | 41.5±3.5 | —2.3 | 0.7 |
| | 42 | 1886– 1 | 109 | 90 | 199 | 45.2±2.4 | +1.4 | 0.6 |
| | $F_3$ | $F_4$ | | | | | | |
| | 1876–17 | 1973– 1 | 180 | 129 | 309 | 41.7±1.9 | —2.1 | 1.1 |
| | | 11 | 183 | 155 | 338 | 45.9±1.8 | +2.1 | 1.2 |
| | | 12 | 227 | 179 | 406 | 44.1±1.7 | +0.3 | 0.2 |
| | | 13 | 58 | 47 | 105 | 44.8±3.3 | +1.0 | 0.3 |
| | | 14 | 218 | 140 | 358 | 39.1±1.8 | —4.7 | 2.6 |
| | 1962–21 | 2845– 1 | 123 | 106 | 229 | 46.3±2.2 | +2.5 | 1.1 |
| | | 2 | 15 | 14 | 29 | 48.3±6.2 | +4.5 | 0.7 |
| | | 2846– 4 | 129 | 92 | 221 | 41.6±2.3 | —2.2 | 1.0 |
| | | 8 | 62 | 59 | 121 | 48.8±3.0 | +5.0 | 1.7 |
| | | 11 | 70 | 55 | 125 | 44.0±3.0 | +0.2 | 0.1 |
| | Total, 24 progenies | | 2,525 | 1,911 | 4,436 | 43.1±0.5 | —0.7 | 1.4 |

* Probable errors are based on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for group I, and 56.25 and 43.75 per cent for group J.

† Deviations are calculated from 25 per cent in group I and 43.8 per cent in group J.

TABLE 6. RECORDS OF ALEURONE COLOR IN THIRTY-SIX $F_4$ PROGENIES OF COLORED $F_3$ INDIVIDUALS OF GROUPS D, F, AND G, FIGURE 71 AND TABLE 4

| $F_3$ ratios | Group | $F_3$ | | $F_4$ | Number of individuals | | | Per cent of colorless individuals* | Deviation† | Dev./P. E. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Pedigree no. | Per cent of colorless individuals | Pedigree no. | Colored | Colorless | Total | | | |
| 3:1 (Group D) | 1 | 1983–101 | 24.0 | 2870– 2 | 220 | 0 | 220 | 0 | ..... | ..... |
| | 2 | 1983–44 | 22.8 | 2872– 4 | 149 | 40 | 189 | 21.2±2.1 | —3.8 | 1.8 |
| | | | | 6 | 186 | 70 | 256 | 27.3±1.8 | +2.3 | 1.3 |
| | | 74 | 23.7 | 2876– 1 | 411 | 133 | 544 | 24.4±1.3 | —0.6 | 0.5 |
| | | | | 5 | 45 | 13 | 58 | 22.4±3.8 | —2.6 | 0.7 |
| | | 101 | 24.0 | 2870– 1 | 160 | 54 | 214 | 25.2±2.0 | +0.2 | 0.1 |
| | | Total, 5 progenies..... | | | 951 | 310 | 1,261 | 24.6±0.8 | —0.4 | 0.5 |
| 9:7 (Group F) | 3 | 1984– 3 | 49.3 | 2866– 1 | 53 | 15 | 68 | 22.1±3.5 | —2.9 | 0.8 |
| | | | | 6 | 186 | 55 | 241 | 22.8±1.9 | —2.2 | 1.2 |
| | | 1983–87 | 51.2 | 2867– 3 | 179 | 74 | 253 | 29.2±1.8 | +4.2 | 2.3 |
| | | | | 6 | 182 | 66 | 248 | 26.6±1.9 | +1.6 | 0.8 |
| | | Total, 4 progenies..... | | | 600 | 210 | 810 | 25.9±1.0 | +0.9 | 0.9 |
| | 4 | 1984– 3 | 49.3 | 2866– 4 | 48 | 45 | 93 | 48.4±3.5 | +4.6 | 1.3 |
| | | 1983–87 | 51.2 | 2867– 7 | 108 | 80 | 188 | 42.6±2.4 | —1.2 | 0.5 |
| | | | | 8 | 56 | 55 | 111 | 49.5±3.2 | +5.7 | 1.8 |
| | | Total, 3 progenies..... | | | 212 | 180 | 392 | 45.9±1.7 | +2.1 | 1.2 |
| | 5 | 1983–23 | 54.5 | 2864– 1 | 162 | 0 | 162 | 0 | ..... | ..... |
| | | | | 5 | 196 | 0 | 196 | 0 | ..... | ..... |
| | | Total, 2 progenies..... | | | 358 | 0 | 358 | 0 | ..... | ..... |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 27:37 (Group G) | 6 | 1983-23 | 54.5 | 2863-11 | 194 | 62 | 256 | 24.2±1.8 | —0.8 | 0.4 |
| | | | | 2864- 3 | 173 | 60 | 233 | 25.8±1.9 | +0.8 | 0.4 |
| | | 36 | 49.1 | 2860-14 | 404 | 150 | 554 | 27.1±1.2 | +2.1 | 1.7 |
| | | | | 2861- 1 | 307 | 95 | 402 | 23.6±1.5 | —1.4 | 0.9 |
| | | | | 4 | 227 | 86 | 313 | 27.5±1.7 | +2.5 | 1.5 |
| | | | | 8 | 328 | 118 | 446 | 26.5±1.4 | +1.5 | 1.1 |
| | | Total, 6 progenies..... | | | 1,633 | 571 | 2,204 | 25.9±0.6 | +0.9 | 1.5 |
| | 7 | 1983-23 | 54.5 | 2863-13 | 30 | 19 | 49 | 38.8±4.8 | —5.0 | 1.0 |
| | | 36 | 49.1 | 2859- 1 | 39 | 34 | 73 | 46.6±3.9 | +2.8 | 0.7 |
| | | | | 3 | 170 | 138 | 308 | 44.8±1.9 | +1.0 | 0.5 |
| | | | | 8 | 97 | 76 | 173 | 43.9±2.5 | +0.1 | 0 |
| | | | | 13 | 131 | 115 | 246 | 46.7±2.1 | +2.9 | 1.4 |
| | | | | 2860- 1 | 124 | 95 | 219 | 43.4±2.3 | —0.4 | 0.2 |
| | | | | 4 | 203 | 161 | 364 | 44.2±1.8 | +0.4 | 0.2 |
| | | | | 6 | 226 | 174 | 400 | 43.5±1.7 | —0.3 | 0.2 |
| | | | | 7 | 239 | 198 | 437 | 45.3±1.6 | +1.5 | 0.9 |
| | | | | 8 | 166 | 144 | 310 | 46.5±1.9 | +2.7 | 1.4 |
| | | | | 2861- 6 | 31 | 28 | 59 | 47.5±4.4 | +3.7 | 0.8 |
| | | Total, 11 progenies..... | | | 1,456 | 1,182 | 2,638 | 44.8±0.7 | +1.0 | 1.4 |
| | 8 | 1983-23 | 54.5 | 2863- 2 | 33 | 41 | 74 | 55.4±3.9 | —2.4 | 0.6 |
| | | | | 2864- 2 | 15 | 23 | 38 | 60.5±5.4 | +2.7 | 0.5 |
| | | | | 4 | 86 | 115 | 201 | 57.2±2.3 | —0.6 | 0.3 |
| | | 36 | 49.1 | 2859- 9 | 60 | 73 | 133 | 54.9±2.9 | —2.9 | 1.0 |
| | | | | 10 | 55 | 103 | 158 | 65.2±2.7 | +7.4 | 2.7 |
| | | | | 2860-16 | 220 | 322 | 542 | 59.4±1.4 | +1.6 | 1.1 |
| | | | | 2861- 7 | 138 | 198 | 336 | 58.9±1.8 | +1.1 | 0.6 |
| | | Total, 7 progenies..... | | | 607 | 875 | 1,482 | 59.0±0.9 | +1.2 | 1.3 |

* Probable errors are based on the assumption that $p$ and $q$ are, respectively, 75 and 25 per cent for groups 2, 3, and 6; 56.25 and 43.75 per cent for groups 4 and 7; and 42.1875 and 57.8125 for group 8.

† Deviations are calculated from 25 per cent in groups 2, 3, and 6; from 43.8 per cent in groups 4 and 7; and from 57.8 per cent in group 8.

TABLE 7. RECORDS OF ALEURONE COLOR IN THIRTY-THREE $F_2$ PROGENIES OF CROSSES BETWEEN COLORLESS ALEURONE TESTERS AND HOMOZYGOUS COLORED ALEURONE TYPES

| Group | Pedigree nos. | | Number of individuals | | | Per cent of colorless individuals* | Anomalous individuals |
|---|---|---|---|---|---|---|---|
| | $F_1$ | $F_2$ | Colored | Colorless | Total | | |
| | *a C R x A C R* | | | | | | |
| | 6876-11 x 6833-11 | 7543- 6 | 226 | 79 | 305 | 25.9±1.7 | ..... |
| | | 8 | 308 | 80 | 388 | 20.6±1.5 | ..... |
| | 13 x 6839- 8 | 7552- 1 | 300 | 102 | 402 | 25.4±1.5 | ..... |
| | | 8 | 194 | 54 | 248 | 21.8±1.9 | ..... |
| 1 | | 10 | 193 | 67 | 260 | 25.8±1.8 | ..... |
| | 15 x 6846- 1 | 7557- 4 | 328 | 108 | 436 | 24.8±1.4 | ..... |
| | | 6 | 348 | 121 | 469 | 25.8±1.3 | ..... |
| | *A C R x a C R* | | | | | | |
| | 6837-10 x 6878- 3 | 7546- 2 | 427 | 132 | 559 | 23.6±1.2 | ..... |
| | | 3 | 443 | 120 | 563 | 21.3±1.2 | 2 |
| | Total, 9 progenies..... | | 2,767 | 863 | 3,630 | 23.8±0.5 | 2 |
| | *A c R x A C R* | | | | | | |
| | 6852- 4 x 6833-11 | 7544- 1 | 214 | 71 | 285 | 24.9±1.7 | 2 |
| | | 10 | 233 | 68 | 301 | 22.6±1.7 | 3 |
| | 6854-16 x 6839- 1 | 7553- 3 | 176 | 63 | 239 | 26.4±1.9 | ..... |
| | | 9 | 269 | 110 | 379 | 29.0±1.5 | ..... |
| | 12 x 6846- 1 | 7559- 4 | 267 | 98 | 365 | 26.8±1 5 | ..... |
| 2 | | 6 | 367 | 113 | 480 | 23.5±1.3 | ..... |
| | | 9 | 262 | 114 | 376 | 30.3±1.5 | ..... |
| | 6855- 9 x 6837-14 | 7547- 1 | 176 | 63 | 239 | 26.4±1.9 | ..... |
| | | 4 | 388 | 119 | 507 | 23.5±1.3 | ..... |
| | | 10 | 322 | 102 | 424 | 24.1±1.4 | ..... |
| | Total, 10 progenies..... | | 2,674 | 921 | 3,595 | 25.6±0.5 | 5 |
| | *A C r x A C R* | | | | | | |
| | 6866-11 x 6833-11 | 7545- 4 | 335 | 127 | 462 | 27.5±1.4 | ..... |
| | | 5 | 202 | 73 | 275 | 26.5±1.8 | ..... |
| | 22 x 6838- 5 | 7560- 2 | 249 | 89 | 338 | 26.3±1.6 | ..... |
| | | 4 | 278 | 92 | 370 | 24.9±1.5 | ..... |
| | | 5 | 273 | 71 | 344 | 20.6±1.6 | ..... |
| | | 7 | 236 | 86 | 322 | 26.7±1.6 | ..... |
| 3 | | 7561- 3 | 215 | 89 | 304 | 29.3±1.7 | ..... |
| | 6867- 4 x 6846- 1 | 7558- 1 | 296 | 125 | 421 | 29.7±1.4 | ..... |
| | | 3 | 259 | 107 | 366 | 29.2±1.5 | ..... |
| | *A C R x A C r* | | | | | | |
| | 6839-10 x 6866-23 | 7554- 3 | 307 | 116 | 423 | 27.4±1.4 | ..... |
| | | 4 | 270 | 97 | 367 | 26.4±1.5 | ..... |
| | | 6 | 257 | 112 | 369 | 30.4±1.5 | ..... |
| | 6837- 4 x 6873- 6 | 7549- 7 | 340 | 131 | 471 | 27.8±1.4 | ..... |
| | | 10 | 377 | 128 | 505 | 25.3±1.3 | ..... |
| | Total, 14 progenies..... | | 3,894 | 1,443 | 5,337 | 27.0±0.4 | 0 |

* Probable errors are based on the assumption that $p$ and $q$ equal 75 and 25 per cent, respectively.

TABLE 8. RECORDS OF ALEURONE COLOR IN $F_1$ OF INTERCROSSES OF COLORLESS ALEURONE TESTERS, *a C R*, *A c R*, AND *A C r*

| Group | Pedigree nos. | Number of individuals* | | |
|---|---|---|---|---|
| | | Colored | Colorless | Anomalous |
| 1 | *a C R* x *a C R* | | | |
| | 6879– 3 x 6876– 4 | 0 | 430 | ..... |
| | 7502– 3 x 7704– 7 | 0 | 320 | ..... |
| | 7503– 3 x 7505– 3 | 1 | 160 | ..... |
| | 3 x 7504– 1 | 0 | 130 | ..... |
| | 7505– 2 x 17 | 0 | 310 | ..... |
| | 1 x 7706– 7 | 0 | 80 | ..... |
| | 7706– 7 x 7502–10 | 0 | 460 | ..... |
| | Total, 7 progenies | 1 | 1,890 | 0 |
| 2 | *A c R* x *A c R* | | | |
| | 6854–19 x 6852–14 | 0 | 180 | ..... |
| | 6855–20 x 2 | 0 | 370 | ..... |
| | 6858–13 x 14 | 0 | 170 | ..... |
| | 6861– 4 x 6882– 5 | 1 | 230 | ..... |
| | 6882– 9 x 6857–26 | 0 | 210 | ..... |
| | 7304–12 x 7508– 1 | 0 | 390 | ..... |
| | 7511– 1 x 7507– 3 | 0 | 90 | ..... |
| | 7512– 6 x 7510–10 | 3 | 370 | ..... |
| | 7514– 3 x 7507– 3 | 0 | 350 | ..... |
| | Total, 9 progenies | 4 | 2,360 | 0 |
| 3 | *A C r* x *A C r* | | | |
| | 6825– 6 x 6872– 4 | 0 | 10 | ..... |
| | 10 x 4 | 0 | 10 | ..... |
| | 6869– 5 x 6871– 3 | 0 | 450 | ..... |
| | 9 x 6867– 2 | 0 | 400 | ..... |
| | 6871–40 x 6869– 9 | 0 | 120 | ..... |
| | 6875–10 x 1 | 0 | 190 | ..... |
| | 6875– 6 x 6871–36 | 0 | 260 | ..... |
| | 6864–20 x 23 | 0 | 450 | ..... |
| | 7222–16 x 7226– 3 | 0 | 280 | ..... |
| | 17 x 7518– 1 | 0 | 130 | ..... |
| | 7516–23 x 7226– 3 | 0 | 250 | ..... |
| | 7517– 1 x 7734– 3 | 0 | 480 | ..... |
| | 7518– 3 x 4 | 0 | 460 | ..... |
| | 8 x 1 | 0 | 410 | ..... |
| | Total, 14 progenies | 0 | 3,900 | 0 |

* Approximate numbers. See table 3, footnote.

TABLE 8 (*continued*)

| Group | Pedigree nos. | Number of individuals* | | |
|---|---|---|---|---|
| | | Colored | Colorless | Anomalous |
| 4 | *a C R x A c R* | | | |
| | 6876–11 x 6854–13 | 490 | 0 | 1 |
| | 6877–14 x 6857– 5 | 160 | 0 | 1 |
| | 6878–31 x 5 | 360 | 1 | 3 |
| | 4 x 6861– 2 | 70 | 0 | . . . |
| | 6879– 1 x 6854–23 | 640 | 2 | 6 |
| | 9 x 6857– 5 | 350 | 0 | 1 |
| | 9 x 6882– 5 | 540 | 0 | 14 |
| | *A c R x a C R* | | | |
| | 6856–15 x 6879– 1 | 100 | 0 | . . . |
| | 7304– 7 x 7503– 2 | 510 | 0 | . . . |
| | 7509–26 x 7502–10 | 220 | 0 | . . . |
| | 7512– 2 x 7503– 4 | 560 | 4 | . . . |
| | 7514– 6 x 7504–14 | 440 | 0 | . . . |
| | Total, 12 progenies | 4,440 | 7 | 26 |
| 5 | *a C R x A C r* | | | |
| | 6876–10 x 6875– 1 | 480 | 1 | 1 |
| | 6877– 1 x 6867– 2 | 90 | 0 | . . . |
| | 6878–24 x 6871–36 | 130 | 2 | . . . |
| | 6879– 5 x 6867– 2 | 670 | 1 | 1 |
| | 7502–13 x 7517–17 | 660 | 1 | . . . |
| | 7504– 6 x 5 | 410 | 0 | . . . |
| | 7505– 4 x 7315– 3 | 70 | 0 | . . . |
| | *A C r x a C R* | | | |
| | 6870–22 x 6877–17 | 360 | 0 | . . . |
| | 7226– 4 x 7503– 3 | 240 | 0 | . . . |
| | 7516–62 x 7504– 1 | 40 | 1 | . . . |
| | 7517– 3 x 7502–10 | 520 | 0 | . . . |
| | Total, 11 progenies | 3,670 | 6 | 2 |
| 6 | *A c R x A C r* | | | |
| | 6851– 7 x 6869– 1 | 100 | 0 | 2 |
| | 6852–10 x 6866–20 | 410 | 0 | . . . |
| | 6854– 8 x 6870– 3 | 30 | 0 | . . . |
| | 9 x 6871–23 | 20 | 0 | . . . |
| | 6855–29 x 39 | 270 | 2 | . . . |
| | 34 x 6870– 3 | 30 | 1 | . . . |
| | 6856– 8 x 6871–39 | 230 | 0 | . . . |

* Approximate numbers. See table 3, footnote.

TABLE 8 (*concluded*)

| Group | Pedigree nos. | Number of individuals* | | |
|---|---|---|---|---|
| | | Colored | Colorless | Anomalous |
| 6 (*concluded*) | *A c R x A C r (concluded)* | | | |
| | 6857- 1 x 6869- 1 | 220 | 0 | |
| | 3 x 6871 41 | 210 | 0 | |
| | 6860- 8 x 6869 1 | 390 | 0 | |
| | 13 x 6871 39 | 300 | 1 | |
| | 6882- 5 x 6866 10 | 230 | 0 | |
| | 8 x 6875 11 | 270 | 0 | |
| | 7304 18 x 7518 1 | 430 | 0 | |
| | 7506 1 x 7226- 3 | 210 | 0 | |
| | 7508- 1 x 7734- 4 | 430 | 0 | |
| | 5 x 7734 1 | 350 | 2 | |
| | 7514-10 x 7517- 5 | 420 | 1 | |
| | 15 x 7519-16 | 230 | 0 | |
| | *A C r x A c R* | | | |
| | 6825- 8 x 6852- 2 | 230 | 0 | |
| | 12 x 2 | 70 | 0 | |
| | 6867- 1 x 2 | 80 | 1 | |
| | 1 x 6857- 5 | 520 | 0 | |
| | 6870- 5 x 6859-14 | 90 | 0 | |
| | 12 x 6854-13 | 480 | 0 | |
| | 13 x 6882 5 | 360 | 1 | |
| | 6873- 6 x 6852-14 | 190 | 0 | 2 |
| | 6875-11 x 6854-13 | 220 | 0 | |
| | 7222-17 x 7507- 1 | 150 | 0 | |
| | Total, 29 progenies | 7,170 | 9 | 4 |

* Approximate numbers. See table 3, footnote.

TABLE 9. RECORDS OF ALEURONE COLOR IN FOURTEEN $F_2$ PROGENIES OF INTERCROSSES BETWEEN COLORLESS ALEURONE TESTERS GIVING COLORED SEEDS IN $F_1$

| Group | Pedigree nos. | | Number of individuals | | | Per cent of colorless individuals* | Anomalous individuals |
|---|---|---|---|---|---|---|---|
| | $F_1$ | $F_2$ | Colored | Colorless | Total | | |
| | *a C R* x *A c R* | | | | | | |
| 1 | 6876-11 x 6854-13 | 7539- 2 | 268 | 190 | 458 | 41.5±1.6 | ..... |
| | | 8 | 272 | 186 | 458 | 40.6±1.6 | ..... |
| | 6879- 1 x 6854-23 | 7540- 1 | 357 | 277 | 634 | 43.7±1.3 | 4 |
| | | 3 | 115 | 75 | 190 | 39.5±2.4 | 1 |
| | | 4 | 141 | 114 | 255 | 44.7±2.1 | ..... |
| | Total, 5 progenies..... | | 1,153 | 842 | 1,995 | 42.2±0.7 | 5 |
| | *a C R* x *A C r* | | | | | | |
| 2 | 6876-10 x 6875- 1 | 7541- 2 | 284 | 192 | 476 | 40.3±1.5 | ..... |
| | | 5 | 258 | 227 | 485 | 46.8±1.5 | ..... |
| | | 7 | 306 | 237 | 543 | 43.6±1.4 | ..... |
| | 6879- 5 x 6867- 2 | 7542- 1 | 135 | 118 | 253 | 46.6±2.1 | ..... |
| | | 7 | 182 | 140 | 322 | 43.5±1.9 | ..... |
| | Total, 5 progenies..... | | 1,165 | 914 | 2,079 | 44.0±0.7 | 0 |
| | *A c R* x *A C r* | | | | | | |
| 3 | 6855-29 x 6871-39 | 7537- 8 | 21 | 16 | 37 | 43.2±5.5 | ..... |
| | 6852-10 x 6866-20 | 7538- 1 | 92 | 88 | 180 | 48.9±2.5 | ..... |
| | | 5 | 216 | 193 | 409 | 47.2±1.7 | ..... |
| | 6852- 2 x 6825- 8 | 7322- 2 | 146 | 114 | 260 | 43.8±2.1 | ..... |
| | Total, 4 progenies..... | | 475 | 411 | 886 | 46.4±1.1 | 0 |

* Probable errors are based on the assumption that $p$ and $q$ equal 56.25 and 43.75 per cent, respectively.

TABLE 10. RECORDS OF ALEURONE COLOR IN $F_1$ OF CROSSES OF COLORLESS ALEURONE TESTERS, *a C R*, *A c R*, AND *A C r*, WITH VARIOUS OTHER TYPES OF COLORLESS ALEURONE

| Group | Aleurone tester | Pedigree nos. | Number of individuals | | |
|---|---|---|---|---|---|
| | | | Colored | Colorless | Anomalous |
| 1 | *a C R* | 6880– 3 x 6876–10 | 10 | 0 | ..... |
| | *A c R* | 6855–24 x 6880– 2 | 0 | 160 | ..... |
| | *A C r* | 6880– 3 x 6866–15 | 0 | 20 | ..... |
| | | 6866–22 x 6880– 2 | 0 | 370 | ..... |
| | | 6875– 8 x 2 | 0 | 150 | ..... |
| | 6880 = *A c r* | | | | |
| 2 | *a C R* | 6881– 2 x 6878–37 | 0 | 200 | ..... |
| | | 6879– 7 x 6881– 3 | 0 | 410 | ..... |
| | *A c R* | 6856–24 x 6881 3 | 80 | 1 | 1 |
| | *A C r* | 6881– 9 x 6869– 5 | 0 | 290 | ..... |
| | *a C R* | 7531– 6 x 7503– 2 | 1 | 340 | ..... |
| | *A c R* | 7531– 5 x 7510– 9 | 140 | 0 | ..... |
| | | 9 x 7 | 360 | 0 | ..... |
| | *A C r* | 7531– 3 x 7516–42 | 0 | 40 | ..... |
| | | 8 x 7518– 4 | 0 | 290 | ..... |
| | 6881, 7531 = *a C r* | | | | |
| 3 | *A c R* | 7513–10 x 7525– 1 | 2 | 580 | ..... |
| | *A C r* | 7519–32 x 1 | 590 | 0 | ..... |
| | *A c R* | 7506–42 x 7526– 3 | 0 | 240 | ..... |
| | *A C r* | 7507–15 x 10 | 0 | 210 | ..... |
| | | 7519– 2 x 7526–10 | 240 | 0 | ..... |
| | 7525, 7526 = *a c R* (*a a* indicated by plant color) | | | | |
| 4 | *a C R* | 6879– 6 x 6885–12 | 0 | 600 | ..... |
| | | 6885–20 x 6879– 1 | 0 | 60 | ..... |
| | *A c R* | 6885– 3 x 6852– 3 | 0 | 280 | ..... |
| | | 12 x 6857– 2 | 0 | 120 | ..... |
| | | 6856–11 x 6885–12 | 0 | 240 | ..... |
| | *A C r* | 6869–10 x 6885–12 | 0 | 260 | ..... |
| | | 6885– 7 x 6869– 5 | 0 | 110 | ..... |
| | | 23 x 6866–15 | 1 | 290 | ..... |
| | | 4 x 6875–18 | 0 | 110 | ..... |
| | | 21 x 11 | 0 | 210 | ..... |
| | 6885 = *a c r* | | | | |

TABLE 11. RECORDS OF ALEURONE COLOR IN $F_2$ OF CROSSES OF *a C r* WITH *A c R* AND OF *a c r* WITH *A C R*

| Pedigree nos. | | Number of individuals | | | Per cent of colorless individuals* |
|---|---|---|---|---|---|
| $F_1$ | $F_2$ | Colored | Colorless | Total | |
| *A c R* x *a C r* | | | | | |
| 6856–24 x 6881–3 | 7536–1 | 296 | 366 | 662 | 55.3±1.3 |
| | 6 | 80 | 121 | 201 | 60.2±2.3 |
| *A C R* x *a c r* | | | | | |
| 6834–12 x 6885–1 | 7534–3 | 116 | 169 | 285 | 59.3±2.0 |
| 6837–10 x 2 | 7535–1 | 192 | 244 | 436 | 56.0±1.6 |
| | 6 | 185 | 236 | 421 | 56.1±1.6 |
| | 8 | 156 | 219 | 375 | 58.4±1.7 |
| 6837–14 x 6885–2 | 7551–2 | 155 | 222 | 377 | 58.9±1.7 |
| Total, 7 progenies | ..... | 1,180 | 1,577 | 2,757 | 57.2±0.6 |

* Probable errors are based on the assumption that $p$ and $q$ equal 42.1875 and 57.8125 per cent, respectively.

TABLE 12. RECORDS OF ALEURONE COLOR IN CROSSES OF *A a C c R r* $F_1$ PLANTS, WHOSE $F_2$ PROGENIES ARE GIVEN IN TABLE 11, WITH *A*, *C*, AND *R* TESTERS AND WITH *a c r* PLANTS

| Group | Pedigree nos. | Number of individuals | | | Per cent of colorless individuals* |
|---|---|---|---|---|---|
| | | Colored | Colorless | Total | |
| 1 Crosses with *a C R* | 7536– 5 x 7502–13 | 320 | 333 | 653 | 51.0±1.3 |
| | 7503– 1 x 7535– 8 | 259 | 248 | 507 | 48.9±1.5 |
| | Total, 2 crosses | 579 | 581 | 1,160 | 50.1±1.0 |
| 2 Crosses with *A c R* | 7536– 3 x 7510– 7 | 382 | 398 | 780 | 51.0±1.2 |
| | 7535– 2 x 7 | 216 | 240 | 456 | 52.6±1.6 |
| | 7509–33 x 7535– 8 | 180 | 158 | 338 | 46.7±1.8 |
| | Total, 3 crosses | 778 | 796 | 1,574 | 50.6±0.9 |
| 3 Crosses with *A C r* | 7516–73 x 7536– 6 | 105 | 98 | 203 | 48.3±2.4 |
| | 70 x 7535– 8 | 117 | 123 | 240 | 51.2±2.2 |
| | 7535– 4 x 7516–42 | 301 | 305 | 606 | 50.3±1.4 |
| | Total, 3 crosses | 523 | 526 | 1,049 | 50.1±1.0 |

* Probable errors are based on the assumption that $p$ and $q$ are each 50 per cent for groups 1, 2, and 3, and 12.5 and 87.5 per cent, respectively, for group 4.

TABLE 12 (*concluded*)

| Group | Pedigree nos. | Number of individuals | | | Per cent of colorless individuals* |
|---|---|---|---|---|---|
| | | Colored | Colorless | Total | |
| 4 Crosses with *a c r* | 7536– 2 x 7520– 2..... | 89 | 531 | 620 | 85.6±0.9 |
| | 6 x 3..... | 79 | 559 | 638 | 87.6±0.9 |
| | 7534– 5 x 6..... | 39 | 311 | 350 | 88.9±1.2 |
| | 7535– 1 x 3..... | 66 | 390 | 456 | 85.5±1.0 |
| | Total, 4 crosses..... | 273 | 1,791 | 2,064 | 86.8±0.5 |

* Probable errors are based on the assumption that $p$ and $q$ are each 50 per cent for groups 1, 2, and 3, and 12.5 and 87.5 per cent, respectively, for group 4.

TABLE 13. RECORDS OF ALEURONE COLOR IN CROSSES OF *A A C c R r* $F_1$ PLANTS, WHOSE $F_2$ PROGENIES ARE REPORTED IN PART IN TABLE 9, WITH ALEURONE TESTERS AND WITH *a c r*

| Group | Pedigree nos. | Number of individuals | | | Per cent of colorless individuals* |
|---|---|---|---|---|---|
| | | Colored | Colorless | Total | |
| 1 Cross with *a C R* | 7503– 2 x 7538– 8..... | 320 | 0 | 320 | 0 |
| 2 Crosses with *A c R* | 7510– 9 x 7538– 8..... | 150 | 157 | 307 | 51.1±1.9 |
| | 7318– 6 x 7304–15..... | 193 | 196 | 389 | 50.4±1.7 |
| | 7 x 15..... | 151 | 160 | 311 | 51.4±1.9 |
| | Total, 3 crosses..... | 494 | 513 | 1,007 | 50.9±1.1 |
| 3 Crosses with *A C r* | 7318– 1 x 7317– 4..... | 72 | 90 | 162 | 55.6±2.6 |
| | 4 x 6..... | 109 | 112 | 221 | 50.7±2.3 |
| | 7317– 6 x 7318– 4..... | 76 | 91 | 167 | 54.5±2.6 |
| | 6 x 7322– 4..... | 106 | 103 | 209 | 49.3±2.3 |
| | 7322– 3 x 7317– 4..... | 176 | 177 | 353 | 50.1±1.8 |
| | 4 x 6..... | 152 | 134 | 286 | 46.9±2.0 |
| | 5 x 7323– 3..... | 153 | 138 | 291 | 47.4±2.0 |
| | Total, 7 crosses..... | 844 | 845 | 1,689 | 50.0±0.8 |
| 4 Cross with *a c r* | 7538– 7 x 7520– 2..... | 153 | 388 | 541 | 71.7±1.3 |

* Probable errors are based on the assumption that $p$ and $q$ are each 50 per cent for groups 2 and 3, and 25 and 75 per cent, respectively, for group 4.

TABLE 14. RECORDS OF ALEURONE COLOR IN $F_2$ AND $F_3$ FROM AN $F_1$ OF THE GENOTYPE *A A C C Rr*

| Group | Pedigree no. | Number of individuals | | | | | Per cent of colorless individuals | Per cent mottled of total colored individuals* |
|---|---|---|---|---|---|---|---|---|
| | | Colored | | | Colorless | Total | | |
| | | Self | Mottled | Total | | | | |
| 1 $F_2$ progenies | 1868– 1 | 140 | 57 | 197 | 88 | 285 | 30.9 | 28.9±2.3 |
| | 3 | 121 | 45 | 166 | 61 | 227 | 26.9 | 27.1±2.5 |
| | Total, 2 progenies | 261 | 102 | 363 | 149 | 512 | 29.1 | 28.1±1.7 |
| 2 $F_3$ from mottled $F_2$ seeds | 1957– 1 | 57 | 25 | 82 | 24 | 106 | 22.6 | 30.5±3.5 |
| | 3 | 35 | 17 | 52 | 19 | 71 | 26.8 | 32.7±4.4 |
| | 1960–14 | 55 | 20 | 75 | 25 | 100 | 25.0 | 26.7±3.7 |
| | 2833– 1 | 51 | 18 | 69 | 20 | 89 | 22.5 | 26.1±3.8 |
| | 4 | 138 | 50 | 188 | 56 | 244 | 23.0 | 26.6±2.3 |
| | 5 | 65 | 39 | 104 | 31 | 135 | 23.0 | 37.5±3.1 |
| | 2836– 5 | 21 | 10 | 31 | 7 | 38 | 18.4 | 32.3±5.7 |
| | 8 | 37 | 16 | 53 | 17 | 70 | 24.3 | 30.2±4.4 |
| | Total, 8 progenies | 459 | 195 | 654 | 199 | 853 | 23.3 | 29.8±1.2 |
| 3 $F_3$ from self-colored $F_2$ seeds | 1958–20 | 25 | 13 | 38 | 12 | 50 | 24.0 | 34.2±5.2 |
| | 32 | 62 | 17 | 79 | 19 | 98 | 19.4 | 21.5±3.6 |
| | 40 | 124 | 51 | 175 | 63 | 238 | 26.5 | 29.1±2.4 |
| | 53 | 46 | 18 | 64 | 14 | 78 | 17.9 | 28.1±4.0 |
| | 1961– 9 | 105 | 43 | 148 | 51 | 199 | 25.6 | 29.1±2.6 |
| | 11 | 159 | 103 | 262 | 92 | 354 | 26.0 | 39.3±2.0 |
| | 13 | 29 | 11 | 40 | 12 | 52 | 23.1 | 27.5±5.0 |
| | 15 | 30 | 14 | 44 | 14 | 58 | 24.1 | 31.8±4.8 |
| | 2834– 2 | 55 | 23 | 78 | 29 | 107 | 27.1 | 29.5±3.6 |
| | 14 | 45 | 15 | 60 | 16 | 76 | 21.1 | 25.0±4.1 |
| | Total, 10 progenies | 680 | 308 | 988 | 322 | 1,310 | 24.6 | 31.2±1.0 |
| 4 $F_3$ from self-colored $F_2$ seeds | 1958–39 | 45 | 0 | 45 | 0 | 45 | 0 | 0 |
| | 1961–20 | 47 | 0 | 47 | 0 | 47 | 0 | 0 |
| | 34 | 76 | 0 | 76 | 0 | 76 | 0 | 0 |
| | 2834– 7 | 89 | 0 | 89 | 0 | 89 | 0 | 0 |
| | 8 | 63 | 0 | 63 | 0 | 63 | 0 | 0 |
| | 2837– 6 | 21 | 0 | 21 | 0 | 21 | 0 | 0 |
| | Total, 6 progenies | 341 | 0 | 341 | 0 | 341 | 0 | 0 |

* Probable errors are based on the assumption that $p$ and $q$ equal 66.7 and 33.3 per cent, respectively.

TABLE 15. RECORDS OF ALEURONE COLOR IN $F_1$ OF CROSSES OF ALEURONE TESTERS WITH FAMILIES RECORDED IN TABLE 14 AND RELATED FAMILIES

| Group | Pedigree nos. | Number of individuals | | | | | Per cent of colorless individuals | Per cent mottled of total colored individuals |
|---|---|---|---|---|---|---|---|---|
| | | Colored | | | Colorless | Total | | |
| | | Self | Mottled | Total | | | | |
| 1 *A c R* as male parent | 1957– 2 x 1991– 4 | 37 | 40 | 77 | 0 | 77 | 0 | 51.9 |
| | 19 x 4 | 80 | 60 | 140 | 0 | 140 | 0 | 42.8 |
| | 2833– 1 x 2885– 1 | 5 | 7 | 12 | 0 | 12 | 0 | 58.3 |
| | Total, 3 progenies | 122 | 107 | 229 | 0 | 229 | 0 | 46.7 |
| 2 *a C r* as male parent | 1957–19 x 1995–26 | 4 | 0 | 4 | 5 | 9 | 55.6 | 0 |
| | 2833– 4 x 2887–31 | 13 | 0 | 13 | 12 | 25 | 48.0 | 0 |
| | 5 x 2886– 3 | 6 | 0 | 6 | 10 | 16 | 62.5 | 0 |
| | 8 x 7 | 3 | 0 | 3 | 5 | 8 | 62.5 | 0 |
| | 2836– 4 x 2888– 4 | 8 | 0 | 8 | 5 | 13 | 38.5 | 0 |
| | Total, 5 progenies | 34 | 0 | 34 | 37 | 71 | 52.1 | 0 |
| 3 *a C r* as female parent | 2887– 8 x 2834–14 | 0 | 22 | 22 | 16 | 38 | 42.1 | 100 |
| 4 *A c R* as male parent | 1956–30 x 1991–22 | 0 | 80 | 80 | 0 | 80 | 0 | 100 |
| | 2835–11 x 2884–23 | 0 | 95 | 95 | 0 | 95 | 0 | 100 |
| | Total, 2 progenies | 0 | 175 | 175 | 0 | 175 | 0 | 100 |
| 5 *A c R* as female parent | 2885–10 x 2832– 7 | 20 | 0 | 20 | 0 | 20 | 0 | 0 |
| 6 *a C r* as male parent | 1959–15 x 1996–13 | 0 | 0 | 0 | 15 | 15 | 100 | ..... |
| | 2832– 1 x 2888–19 | 0 | 0 | 0 | 29 | 29 | 100 | ..... |
| | 2887– 7 x 2832– 7 | 0 | 0 | 0 | 15 | 15 | 100 | ..... |
| | 2886–13 x 7 | 0 | 0 | 0 | 11 | 11 | 100 | ..... |
| *a C r* as female parent | Total, 4 progenies | 0 | 0 | 0 | 70 | 70 | 100 | ..... |

TABLE 16. RECORDS OF ALEURONE COLOR OF SELFED HOMOZYGOUS COLORED TYPES, AND OF $F_1$ OF RECIPROCAL CROSSES BETWEEN THEM AND ALEURONE TESTERS

| Group | Pedigree nos. | Number of individuals* | | |
|---|---|---|---|---|
| | | Self-colored | Mottled | Anomalous |
| 1 Selfed homozygous colored | 6832–27 | 130 | 0 | |
| | 31 | 350 | 0 | |
| | 6833–11 | 250 | 0 | |
| | 6837– 8 | 380 | 0 | |
| | 12 | 280 | 0 | |
| | 6838– 5 | 260 | 0 | |
| | 6839– 9 | 30 | 0 | |
| | 6841– 3 | 300 | 0 | |
| | 9 | 300 | 0 | |
| | 7600– 8 | 280 | 0 | |
| | Total, 10 progenies | 2,560 | 0 | |
| 2 A tester as female parent | 6878–20 x 6832– 4 | 440 | 0 | |
| | 6876–16 x 6833–11 | 490 | 0 | 1 |
| | 13 x 6839– 8 | 530 | 0 | 1 |
| | Total, 3 progenies | 1,460 | 0 | 2 |
| 3 A tester as male parent | 6832–10 x 6876–10 | 230 | 0 | |
| | 11 x 10 | 240 | 0 | |
| | 6837–10 x 6878– 3 | 540 | 0 | |
| | 6838– 5 x 3 | 260 | 0 | |
| | 6839– 8 x 6876–16 | 160 | 0 | |
| | 7600– 1 x 7504– 5 | 270 | 0 | |
| | Total, 6 progenies | 1,700 | 0 | |
| 4 C tester as female parent | 6851– 6 x 6832– 2 | 410 | 0 | |
| | 6855– 1 x 2 | 360 | 0 | |
| | 6852– 4 x 6833–11 | 230 | 0 | |
| | 6855– 9 x 6837–14 | 290 | 0 | |
| | 6854– 6 x 6838– 5 | 20 | 0 | |
| | 16 x 6839– 1 | 260 | 0 | |
| | 6855–10 x 21 | 190 | 0 | |
| | 7510– 3 x 7600– 1 | 350 | 0 | |
| | Total, 8 progenies | 2,110 | 0 | |

* Approximate numbers. See table 3, footnote.

TABLE 16 (*concluded*)

| Group | Pedigree nos. | Number of individuals* | | |
|---|---|---|---|---|
| | | Self-colored | Mottled | Anomalous |
| 5<br>*C* tester as male parent | 6837–16 x 6852– 3 | 470 | 0 | |
| | 6838– 1 x 6855– 1 | 160 | 0 | |
| | 6839– 3 x 1 | 80 | 0 | |
| | 6840–10 x 6854–17 | 140 | 0 | |
| | 6841–16 x 6852–31 | 470 | 0 | |
| | 7599– 3 x 7506–21 | 240 | 0 | |
| | Total, 6 progenies | 1,560 | 0 | |
| 6<br>*R* tester as female parent | 6866–18 x 6832– 9 | 0 | 470 | |
| | 6870– 1 x 22 | 0 | 420 | |
| | 6875– 1 x 31 | 0 | 110 | |
| | 6866–16 x 6833–11 | 0 | 340 | |
| | 6875– 4 x 6838– 4 | 0 | 30 | |
| | 2 x 5 | 0 | 260 | |
| | 6874– 1 x 6840– 4 | 0 | 210 | |
| | 6871– 1 x 6845– 7 | 0 | 180 | |
| | 7516–33 x 7600– 1 | 0 | 170 | |
| | Total, 9 progenies | 0 | 2,190 | |
| 7<br>*R* tester as male parent | 6832– 2 x 6866–18 | 190 | 0 | |
| | 6833– 4 x 6873– 6 | 120 | 0 | |
| | 10 x 6870– 5 | 200 | 0 | |
| | 6837– 4 x 6873– 6 | 490 | 0 | |
| | 6838–10 x 6866–22 | 20 | 0 | |
| | Total, 5 progenies | 1,020 | 0 | |

* Approximate numbers. See table 3, footnote

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AGRICULTURAL EXPERIMENT STATION

# THE TRANSLOCATION OF CALCIUM IN A SOIL

BENJAMIN DUNBAR WILSON

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# THE TRANSLOCATION OF CALCIUM IN A SOIL

# THE TRANSLOCATION OF CALCIUM IN A SOIL

BENJAMIN DUNBAR WILSON

The presence of calcium in soil is of extreme importance. The action of this element, when applied in different chemical combinations to soil, has been investigated extensively. In spite of the fact that much has been written on the subject of calcium in soil, it is evident from a review of the literature that the movement of calcium in soil has received but little attention. Definite information in relation to the translocation of calcium in soil, under carefully controlled laboratory or field conditions, is unsupplied.

The present investigation was undertaken in an attempt to answer the following questions: (1) Does the calcium applied to a soil move downward or does it remain in the upper few inches of soil? (2) If the calcium does move downward, to what extent does it move?

## REVIEW OF LITERATURE

The only study that has been made on the downward movement of calcium in soils under controlled laboratory conditions, so far as the writer has been able to discover, is that of Broughton (1912).[1] In that experiment the movement of calcium thru sandy, loam, and clay soils was determined, the calcium being applied in different forms. It was found that the movement of calcium thru a soil was governed largely by the physical constitution of the latter, the calcium salts diffusing most rapidly thru a sandy soil, less rapidly thru a loam soil, and only slightly thru a clay soil. Some of the differences which the author reports in the movement of calcium, resulting from the different treatments that were used, might have disappeared had the treatments been repeated a greater number of times; also, the method employed for sampling pots at different intervals necessitated a disturbance of the soils within the pots, which may have resulted in some mechanical movement of calcium.

Several investigators have endeavored to determine the translocation of calcium in field soils by comparing the quantity of calcium found at

[1] Dates in parenthesis refer to *Literature cited*, page 324.

different depths in soils that had received an application of calcium in some form with that in other soils of the same type that had not been treated with any form of calcium. McIntire (1913) analyzed a silty loam soil for calcium at different depths from plats that had received large applications of either calcium oxid or calcium carbonate for a period of thirty years. From a comparison of the calcium found in the treated soil with that found in the soil from adjacent untreated plats, it was concluded that calcium applied in either form at the surface of such soil moves downward very slowly, most of it remaining for years in the surface soil.

The analyses for calcium carbonate in the surface soils and subsoils of Broadbalk and Hoos fields at Rothamsted, which have been made at different times since 1865 as reported by Hall and Miller (1905), show that the subsoils have decreased in calcium, as well as the surface soils, which latter had received large applications of calcium previous to 1865 and which since that time have received yearly, for more than fifty years, the same fertilizer treatments. The results indicate that there has been no accumulation of calcium in the subsoils, altho there seems to be a tendency for an increase in the subsoils where ammonium sulfate has been applied from year to year to the surface soils.

Veitch (1904) studied the downward movement of calcium in soils by determining the soil acidity at varied depths. The results of his investigation showed that when calcium oxid was applied to soils its neutralizing effect was exerted only to the depth to which it was incorporated with the soils during the various processes of preparation and cultivation.

Ames and Schollenberger (1916) present data to show the depth of soil affected by applications of calcium salts. Soils that had been so treated were sampled at different depths and their lime requirements determined by the Hopkins and vacuum methods. The indications were that light applications of lime have considerable effect on the subsoil, at least to a depth of twenty-four inches.

White (1914) reports, from studies made on soils in the field, that calcium does not move horizontally to any considerable degree by diffusion, as soil rich in calcium carbonate was found within eighteen inches of soil distinctly acid.

King (1904) studied the capillary movement of calcium thru soils by filling galvanized cylinders, provided with reservoirs at their bases, with different types of soil. A calcium solution applied at the bottom of the soil columns was permitted to rise by capillarity thru the soils. The results of the experiment tended to show that there was a slight upward movement of calcium.

A comparison of the calcium content of surface and subsurface soils as reported by Smith (1884), Snyder (1899), Ames and Gaither (1913), Shorey, Fry, and Hazen (1917), and others, does not permit of any general conclusion as to whether surface soils or subsurface soils contain the greater amount of calcium. Consequently such a consideration is of no value in a study of the translocation of calcium in soil.

A review of the literature reveals the fact that the studies thus far made on the movement of calcium in soil have been confined almost entirely to field experimentation and have been carried on as side experiments. Results obtained under such conditions are not absolute. The calcium content of soils is not always constant, and in comparing one soil with another this fact alone may lead to erroneous conclusions.

Some investigators have used a method for the determination of lime requirement as a measure of calcium in soils. Such a practice is open to criticism, as a lime requirement is an estimation of the absorptive power of a soil for basic material, not a measure of its calcium content. If calcium should liberate any of the soil bases, such a reaction might account for any decrease found in the lime requirement of the subsoil rather than the actual downward movement of calcium.

As previously stated, very little experimental evidence is available concerning the movement of calcium in soil under carefully controlled conditions. In view of this fact the experiments detailed herein were undertaken.

## EXPERIMENTAL WORK

### *Plan of the investigation*

The investigation consisted of three experiments. These are briefly outlined as follows:

*Experiment 1.*— In the first experiment the translocation of calcium in soil was studied by leaching soil contained in pots with distilled water. The soil was placed in the pots in three layers. In some of the pots

calcium as oxid, and in others calcium as carbonate, was incorporated with the surface layer to test the possible downward movement of this element; in other pots the calcium was mixed with the bottom layer of soil to determine its tendency to move upward. The downward movements of calcium oxid and calcium carbonate, when applied to a soil in medium, large, and excessive amounts and in equivalent quantities of calcium, were collated. The oxid was added as burned limestone, and the carbonate as ground limestone and precipitated calcium carbonate.[2] The state of division of the ground limestone used in the experiment was such that it passed thru a 100-mesh sieve and was held on a 200-mesh sieve. One set of the pots was leached for six months and another set for one year, and at the end of each period the layers of soil in each pot were analyzed for total calcium in contemplation of determining its movement. The experiment was set up in quadruplicate.

*Experiment 2.*— In the second experiment the downward movement of calcium was determined when lots of ground limestone, differing in fineness of division, were applied to the soil in equivalent quantities. Pots filled with soil in three layers were treated with the ground limestone in the top layer, and were leached with distilled water for one year. Limestone of four grades of fineness was used in treating the different pots, the treatment with each grade being repeated four times.

*Experiment 3.*— In the third experiment a comparative study was made of the diffusibility of calcium in a cropped and an uncropped soil. Pots were filled with soil arranged in layers, treated in the surface layer with burned limestone, and leached with distilled water for five months.

### *Soil used*

The soil used in the investigation was a Dunkirk clayey silt loam, a glacial till soil low in organic matter. It comprises the greater part of the soil on the farm of the Cornell University Agricultural Experiment Station, and for this reason it was selected for study. A chemical and a mechanical analysis of this soil, taken from the files of the Department of Soil Technology, Cornell University, follow:

[2] Twice as much ground limestone as burned limestone was applied to the pots. Consequently the quantity of calcium added to the pots treated with ground limestone was slightly in excess of that added to the pots that received a treatment of burned limestone. As it is customary when applying calcium to field soils to follow such a procedure, this ratio was used in experiments 1 and 2.

CHEMICAL ANALYSIS (Bulk)

(An average of the analyses of nine samples)

| | Surface per cent |
|---|---|
| Organic carbon | 1.670 |
| Carbon dioxid | Trace |
| Potassium oxid | 1.740 |
| Calcium oxid | 0.430 |
| Magnesium oxid | 0.450 |
| Sodium oxid | 1.090 |
| Nitrogen | 0.186 |
| Phosphoric anhydrid | 0.123 |

MECHANICAL ANALYSIS

(An average of the analyses of three samples)

| | Surface per cent |
|---|---|
| Fine gravel | 0.5 |
| Coarse sand | 0.8 |
| Medium sand | 0.6 |
| Fine sand | 2.7 |
| Very fine sand | 9.5 |
| Silt | 67.3 |
| Clay | 18.6 |
| Total | 100.0 |

A large quantity of soil was necessary to carry out the experiments, and this was collected at three different times. For convenience, the three soils thus obtained are designated as X, Y, and Z. Soil X was used for experiment 1, soil Y for experiment 2, and soil Z for experiment 3. All three soils were surface soils taken from a roadside adjoining Caldwell Field, a part of the experiment station farm. Each lot was taken to the greenhouse, where it was screened and thoroly mixed, the screenings being discarded. The three soils were in good physical condition.

A representative sample was taken from each of the soils and prepared for analysis. The lime requirement and the calcium content of each are

shown in table 1. The lime requirements were determined by the Veitch (1904) method, and are expressed as parts per million of calcium oxid necessary to correct the acidity in the oven-dried soils. Calcium was determined as recommended by the Ohio Agricultural Experiment Station (Ames and Gaither, 1913). This method was used for all the determinations of calcium that were made thruout the investigation, and consists essentially in fusing the soil with a mixture of sodium and potassium carbonates, precipitating the calcium as calcium oxalate after the removal of silicon, iron, aluminum, and manganese, and titrating the filtered precipitate with a standard solution of potassium permanganate.

TABLE 1. LIME REQUIREMENTS AND PERCENTAGES OF CALCIUM IN SOILS X, Y, AND Z

| Soil | Lime requirement of dry soil (parts per million CaO) | Percentage of total calcium |
|---|---|---|
| X | 900 | 0.328 |
| Y | 800 | 0.300 |
| Z | 1,300 | 0.220 |

*Method of placing soil in pots*

Glazed earthen pots 10 inches in height and $9\frac{1}{2}$ inches in inside diameter were used for the experiments. In each pot was placed thirteen kilograms of soil to form three layers. Of the eighty pots used, seventy-two were filled in the following manner: Into the bottom of each pot was packed five kilograms of soil, which formed the bottom, or third, layer. Over the surface of this layer a piece of wire netting was placed, and on top of it another five-kilogram portion of soil was packed, which constituted the middle, or second, layer. The remaining three kilograms of soil made up the top, or first, layer, which was separated from the middle, or second, layer by a second piece of wire netting. The calcium oxid or calcium carbonate with which the pots were treated was incorporated with the soil making up the first layer before this was placed in the pots.

The remaining eight pots were filled with soil so placed that the upward movement of calcium could be studied. In order to observe this move-

ment, the three-kilogram portions of soil containing the calcium treatments were placed in the bottom of the pots, the top and middle layers consisting of five kilograms each. The layers were separated with wire netting, as described above.

The soil was placed in the pots in layers in order that the calcium-treated soil might be separated from the untreated soil, as well as for a division of the latter, when the pots were opened. The object in dividing the untreated soil into layers was to make possible a comparison of the amounts of calcium in them with reference to their distance from the calcium-treated soil.

*Treatment of pots*

The treatment of the pots in the three experiments may be outlined as follows:

EXPERIMENT 1. TRANSLOCATION OF CALCIUM OXID AND CALCIUM CARBONATE IN SOIL

| Nos. of pots | Treatment (pounds per acre) | Treated layer |
|---|---|---|
| 1, 2, 3, 4 | 3,000 CaO | Top |
| 5, 6, 7, 8 | 3,000 CaO | Top |
| 9, 10, 11, 12 | 9,000 CaO | Top |
| 13, 14, 15, 16 | 9,000 CaO | Top |
| 17, 18, 19, 20 | 15,000 CaO | Top |
| 21, 22, 23, 24 | 15,000 CaO | Top |
| 25, 26, 27, 28 | 15,000 CaO | Bottom |
| 29, 30, 31, 32 | 6,000 $CaCO_3$ | Top |
| 33, 34, 35, 36 | 6,000 $CaCO_3$ | Top |
| 37, 38, 39, 40 | 18,000 $CaCO_3$ | Top |
| 41, 42, 43, 44 | 18,000 $CaCO_3$ | Top |
| 45, 46, 47, 48 | 30,000 $CaCO_3$ | Top |
| 49, 50, 51, 52 | 30,000 $CaCO_3$ | Top |
| 53, 54, 55, 56 | 30,000 $CaCO_3$ | Bottom |

EXPERIMENT 2. DOWNWARD MOVEMENT OF GROUND LIMESTONE OF DIFFERENT DEGREES OF FINENESS THRU SOIL

| Nos. of pots | Treatment (pounds per acre) | Fineness of limestone |
|---|---|---|
| 57, 58, 59, 60 | 9,000 $CaCO_3$ | Thru 10-mesh sieve, held on 32-mesh sieve |
| 61, 62, 63, 64 | 9,000 $CaCO_3$ | Thru 50-mesh sieve, held on 100-mesh sieve |
| 65, 66, 67, 68 | 9,000 $CaCO_3$ | Thru 200-mesh sieve |
| 69, 70, 71, 72 | 9,000 precipitated $CaCO_3$ | |

EXPERIMENT 3. DOWNWARD MOVEMENT OF BURNED LIMESTONE THRU SOIL CROPPED AND UNCROPPED

| Nos. of pots | Treatment (pounds per acre) | |
|---|---|---|
| 73, 74, 75, 76 | 3,000 CaO | Planted (oats) |
| 77, 78, 79, 80 | 3,000 CaO | Unplanted |

*Experiments 1 and 2*

The pots included in experiments 1 and 2 were leached with distilled water equivalent to a yearly rainfall of thirty-six inches. Of these seventy-two pots the following were leached for six months: 5, 6, 7, 8; 13, 14, 15, 16; 21, 22, 23, 24; 33, 34, 35, 36; 41, 42, 43, 44; 49, 50, 51, 52. All the others were leached for one year. The pots leached for six months and those leached for one year received a treatment of twenty-one and forty-two liters of distilled water, respectively. The first treatment of water was applied to the pots on December 22, 1915. The dates and the amounts of the subsequent treatments are shown in table 2.

No water was applied after June 10 to the pots that were leached for six months. These pots were allowed to drain until June 28, which was just six months after the first drainage water had leached from them. The soil was then prepared for the analysis of total calcium as is described later. The pots leached for one year were sampled during the first week in January of 1917.

TABLE 2. DATE OF TREATMENT AND AMOUNT OF DISTILLED WATER APPLIED TO POTS OF EXPERIMENTS 1 AND 2

| No. of treatment | Date | Amount of water applied (in cubic centimeters) | |
|---|---|---|---|
| | | Pots leached for six months | Pots leached for twelve months |
| | 1915 | | |
| 1 | December 22 | 600 | 600 |
| 2 | December 28 | 1,100 | 1,100 |
| | 1916 | | |
| 3 | January 5 | 1,100 | 1,100 |
| 4 | January 8 | 1,100 | 1,100 |
| 5 | January 18 | 800 | 800 |
| 6 | February 14 | 2,400 | 2,400 |
| 7 | February 21 | 800 | 800 |
| 8 | March 6 | 1,600 | 1,600 |
| 9 | March 20 | 1,600 | 1,600 |
| 10 | April 10 | 2,400 | 2,400 |
| 11 | April 24 | 1,600 | 1,600 |
| 12 | May 6 | 1,600 | 1,600 |
| 13 | May 8 | 800 | 800 |
| 14 | May 22 | 1,600 | 1,600 |
| 15 | May 29 | 800 | 800 |
| 16 | June 10 | 1,100 | 1,100 |
| 17 | June 27 | ..... | 1,600 |
| 18 | July 11 | ..... | 1,600 |
| 19 | July 27 | ..... | 1,600 |
| 20 | August 17 | ..... | 2,400 |
| 21 | August 31 | ..... | 1,600 |
| 22 | October 3 | ..... | 2,400 |
| 23 | October 10 | ..... | 800 |
| 24 | October 24 | ..... | 2,400 |
| 25 | November 6 | ..... | 1,600 |
| 26 | November 20 | ..... | 1,600 |
| 27 | November 22 | ..... | 800 |
| 28 | December 1 | ..... | 1,000 |
| 29 | December 10 | ..... | 1,600 |
| Total | ..... | 21,000 | 42,000 |

The drainage from the pots was collected in granite-ware pans, the pots being supported on wooden blocks (fig. 72). The water passed from the bottom of the pots thru round openings about one-half inch in diameter. To prevent the soil from washing thru these apertures, a small paraffined flowerpot was inverted over them before the soil was placed in the pots.

This arrangement afforded excellent drainage. In all the experiments a quartz-sand mulch one-half inch thick, placed on the surface of the soil, prevented evaporation from the pots.

*Bicarbonate* ($HCO_3$) *content of the drainage water*

The amount of bicarbonate ($HCO_3$) contained in the drainage water from the pots leached for one year was determined frequently during the investigation. Samples for analysis were collected in small Erlenmeyer

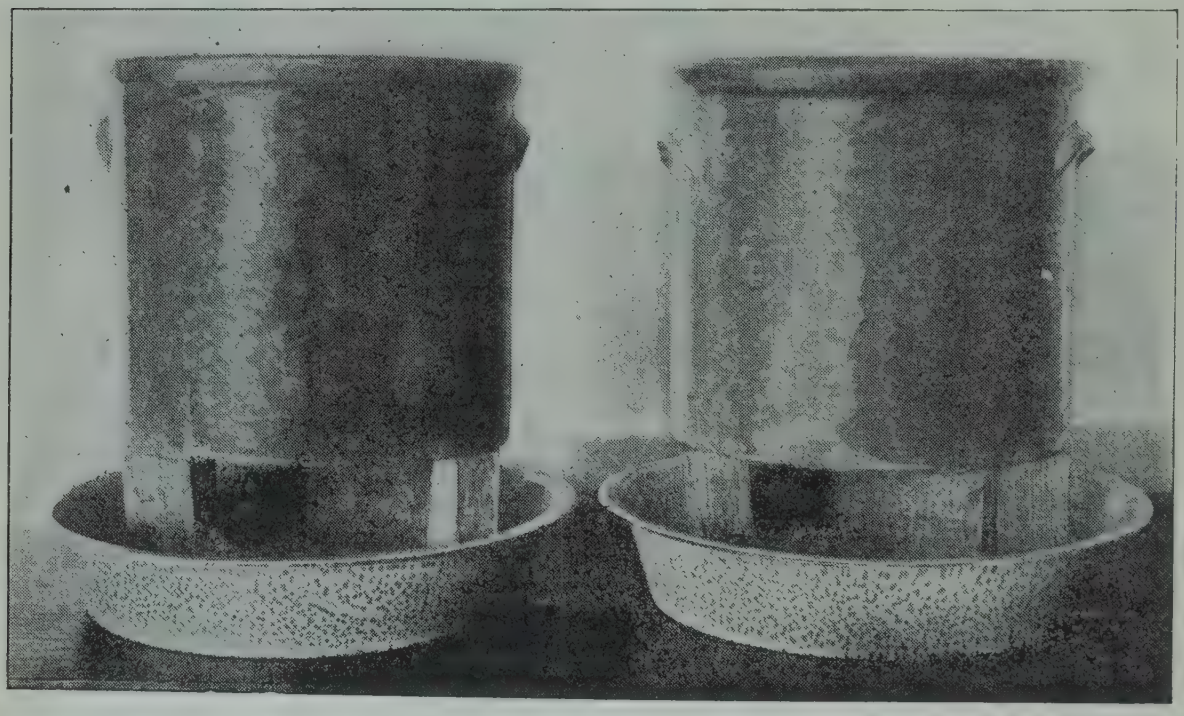

FIG. 72. ARRANGEMENT OF POTS FOR LEACHING

flasks placed in such a manner as to catch the leachings as they came from the pots. It was evident that the bicarbonate content of the solutions would depend somewhat on the amount of percolation that had occurred immediately before the samples were collected for analysis, but this fact was not objectionable as the determinations were made only that some idea of the abundance of the bicarbonate in the leachings might be known.

It is seen from table 3 that the quantities of bicarbonate found in the drainage water from the pots, expressed in parts per million of solution, were sufficient to exert considerable influence on the solubility of the calcium oxid or calcium carbonate with which the pots were treated, and

would lead one to believe that the water applied to the surface of the soil in the pots passed downward thru the soil, not between the soil and the sides of the pots.

TABLE 3. BICARBONATE ($HCO_3$) CONTENT OF DRAINAGE WATER FROM POTS LEACHED WITH DISTILLED WATER FOR ONE YEAR

(Average for similarly treated pots in parts per million of solution)

| Nos. of pots | Treatment (pounds per acre) | Date of collection of drainage water | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Jan. 18 | Feb. 21 | Mar. 20 | Apr. 10 | June 10 | July 11 | Aug. 17 | Oct. 3 | Nov. 6 |
| 1 to 4 | 3,000 CaO | 139 | 112 | 110 | 74 | 162 | 155 | 56 | 42 | 99 |
| 9 to 12 | 9,000 CaO | 125 | 113 | 92 | 82 | 163 | 200 | 74 | 60 | 125 |
| 17 to 20 | 15,000 CaO | 132 | 135 | 139 | 143 | 266 | 279 | 139 | 122 | 188 |
| 29 to 32 | 6,000 $CaCO_3$ | 144 | 112 | 82 | 56 | 121 | 121 | 41 | 39 | 77 |
| 37 to 40 | 18,000 $CaCO_3$ | 165 | 125 | 88 | 71 | 111 | 127 | 51 | 37 | 73 |
| 45 to 48 | 30,000 $CaCO_3$ | 141 | 130 | 113 | 82 | 91 | 82 | 55 | 34 | 60 |
| 57 to 60 | 9,000 $CaCO_3$, thru 10-mesh, held on 32-mesh. | 109 | 92 | 87 | 61 | 81 | 69 | 35 | 28 | 35 |
| 61 to 64 | 9,000 $CaCO_3$, thru 50-mesh, held on 100-mesh | 83 | 71 | 55 | 58 | 53 | 51 | 30 | 21 | 32 |
| 65 to 68 | 9,000 $CaCO_3$, thru 200-mesh | 104 | 100 | 82 | 64 | 94 | 81 | 63 | 32 | 63 |
| 69 to 72 | 9,000 precipitated $CaCO_3$ | 128 | 115 | 91 | 68 | 92 | 81 | 44 | 30 | 39 |

*Experiment 3*

As previously stated, the object of experiment 3 was to determine the effect of a crop on the downward movement of calcium in soil. Eight pots were used for this purpose. The soil was placed in them in three layers, as has been described, and each pot received a treatment of burned limestone equivalent to an application of 3000 pounds to the acre. The experiment was begun on February 18, 1916, when four of the pots were planted to oats. Thirty seeds, which had been previously sterilized with a solution of calcium hypochlorite as suggested by Wilson (1915) were planted in each of the four pots, and the plants were thinned to twelve in a pot on February 26. The crop was harvested on July 18, just five months after it was planted and about the time when the grain

was ripe. There was a good stand of oats on all the planted pots at the time when the crop was harvested.

The four unplanted pots were leached with distilled water at the same rate as were those in the foregoing experiments, which amounted to $17\frac{1}{2}$ liters for five months. It was necessary to add more water to the pots on which the plants were grown, to make up for that lost by transpiration. During the period of growth $25\frac{1}{2}$ liters of distilled water was applied to these pots. In table 4 are shown the amount of water applied to the planted and the unplanted pots from time to time during the experiment, and the dates of its application:

TABLE 4. DATES OF TREATMENT AND AMOUNTS OF DISTILLED WATER APPLIED TO POTS OF EXPERIMENT 3

| No. of treatment | Date | Amount of water applied (in cubic centimeters) | |
|---|---|---|---|
| | | Planted pots | Unplanted pots |
| | 1916 | | |
| 1 | February 19 | 1,000 | 1,000 |
| 2 | February 26 | 800 | 800 |
| 3 | March 5 | 800 | 800 |
| 4 | March 11 | 1,000 | 1,000 |
| 5 | March 24 | 1,000 | 1,000 |
| 6 | April 10 | 1,600 | 1,600 |
| 7 | April 24 | 1,600 | 1,600 |
| 8 | May 4 | 800 | ..... |
| 9 | May 6 | 2,400 | 800 |
| 10 | May 13 | 800 | ..... |
| 11 | May 20 | 2,400 | 1,600 |
| 12 | May 26 | 800 | ..... |
| 13 | June 3 | 2,400 | 1,600 |
| 14 | June 14 | 800 | ..... |
| 15 | June 17 | 2,400 | 1,600 |
| 16 | June 27 | 2,400 | 1,600 |
| 17 | July 8 | 2,500 | 2,500 |
| Total | ..... | 25,500 | 17,500 |

*Method of sampling pots for analysis of calcium*

When the last application of water had drained from the pots, the quartz-sand mulch was removed from the surface of the soil and the pots

were allowed to stand for several days in this condition until the soil was dry enough to be in a good workable condition. A large spatula was used to loosen the soil from the sides of the pots, and by this means it was possible, when inverting the pots, to slide the soil from them as a solid cylindrical mass (fig. 73). In order to guard against the possibility that calcium salts might have been carried down mechanically, during the course of the experiments, between the soil and the sides of the pots, the outside soil of the entire soil mass was removed with a knife, leaving what might be called an inner core of soil. This inner soil core was

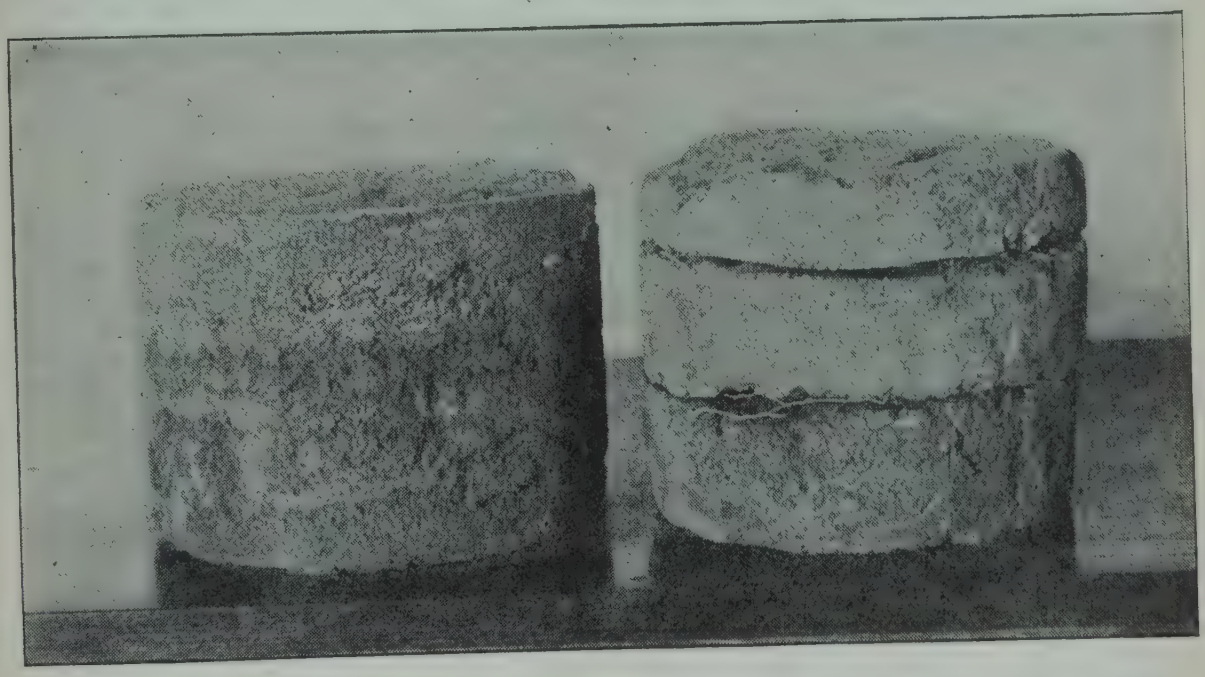

FIG. 73. CORES OF SOIL AS THEY CAME FROM THE POTS, BEFORE AND AFTER DIVISION

divided into three layers by inserting a spatula where the pieces of wire netting had been placed in the soil at the time when the pots were filled (fig. 74). The three layers thus obtained were placed in different receptacles, and a representative sample taken from each of them was air-dried. A portion of this air-dried sample was passed thru a 32-mesh sieve, oven-dried over night, and finally placed in an air-tight eight-ounce bottle, which was set aside until the soil could be analyzed for total calcium according to the method already described (page 304).

None of the soil layers into which some form of calcium had been placed were analyzed for this constituent at the end of the experiments,

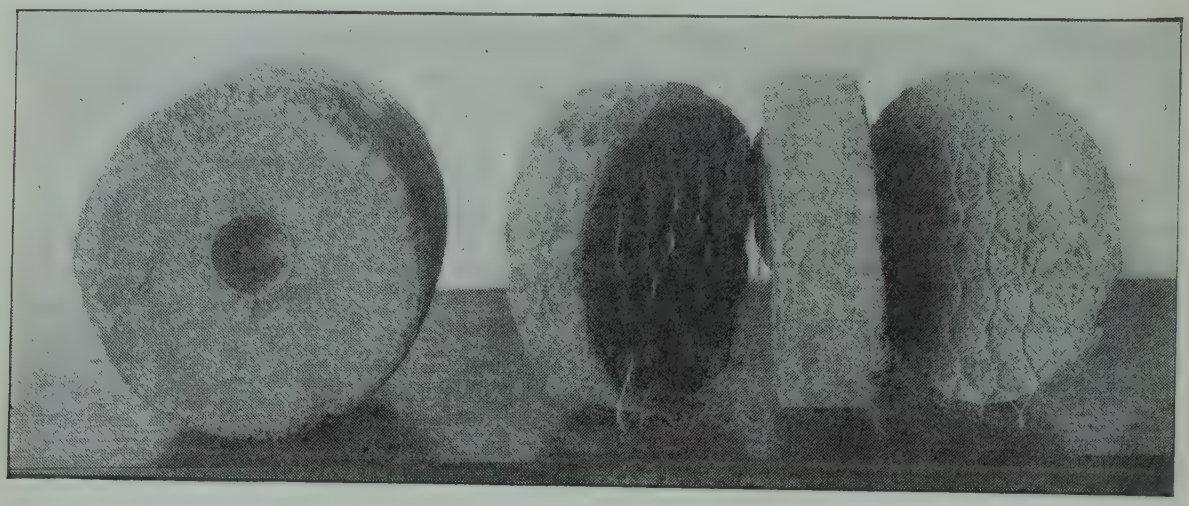

FIG. 74. LEFT: THE BOTTOM OF A CORE OF SOIL.
RIGHT: A CORE OF SOIL DIVIDED INTO ITS THREE LAYERS, SHOWING WIRE NETTING USED

but the amount of calcium present in them at the beginning of the experiments is given in tables 5 to 9. The percentages of calcium found in the analyzed layers at the end of the experiments are taken as an indication of the translocation of this element thru the soil, and are also given in the tables.

TABLE 5. EXPERIMENT 1 — PERCENTAGES OF CALCIUM IN SECOND AND THIRD LAYERS OF SOIL FROM POTS LEACHED WITH DISTILLED WATER FOR SIX MONTHS

(Calcium treatments placed in first layer of soil)

| Treatment (pounds per acre) | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|
| | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | First layer | Second layer | Third layer | Second layer | Third layer | |
| 3,000 CaO | 5 | 0.69 | .37 | .41 | .370±.0098 | .390±.0049 | A |
| | 6 | | .40 | .38 | | | |
| | 7 | | .33 | .39 | | | |
| | 8 | | .38 | .38 | | | |
| 6,000 $CaCO_3$ | 33 | 0.73 | .34 | .28 | .315±.0122 | .295±.0085 | $A_1$ |
| | 34 | | .34 | .28 | | | |
| | 35 | | .27 | .33 | | | |
| | 36 | | .31 | .29 | | | |

TABLE 5 (*concluded*)

| Treatment (pounds per acre) | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|
| | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | First layer | Second layer | Third layer | Second layer | Third layer | |
| 9,000 CaO... | 13 | 1.41 | .37 | .32 | .355±.0122 | .330±.0049 | B |
| | 14 | | .31 | .32 | | | |
| | 15 | | .39 | .33 | | | |
| | 16 | | .35 | .35 | | | |
| 18,000 $CaCO_3$ | 41 | 1.54 | .33 | .33 | .315±.0061 | .325±.0036 | $B_1$ |
| | 42 | | .29 | .31 | | | |
| | 43 | | .32 | .33 | | | |
| | 44 | | .32 | .33 | | | |
| 15,000 CaO.. | 21 | 2.12 | .37 | .37 | .385±.0049 | .365±.0036 | C |
| | 22 | | .38 | .37 | | | |
| | 23 | | .39 | .37 | | | |
| | 24 | | .40 | .35 | | | |
| 30,000 $CaCO_3$ | 49 | 2.33 | .30 | .31 | .310±.0073 | .340±.0122 | $C_1$ |
| | 50 | | .33 | .35 | | | |
| | 51 | | .29 | .32 | | | |
| | 52 | | .32 | .38 | | | |

TABLE 6. EXPERIMENT 1 — PERCENTAGES OF CALCIUM IN SECOND AND THIRD LAYERS OF SOIL FROM POTS LEACHED WITH DISTILLED WATER FOR ONE YEAR

(Calcium treatments placed in first layer of soil)

| Treatment (pounds per acre) | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|
| | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | First layer | Second layer | Third layer | Second layer | Third layer | |
| 3,000 CaO | 1 | 0.69 | .35 | .32 | .340±.0098 | .345±.0122 | D |
| | 2 | | .34 | .36 | | | |
| | 3 | | .37 | .38 | | | |
| | 4 | | .30 | .32 | | | |
| 6,000 $CaCO_3$ | 29 | 0.73 | .32 | .25 | .303±.0103 | .293±.0109 | $D_1$ |
| | 30 | | .32 | .30 | | | |
| | 31 | | .26 | .29 | | | |
| | 32 | | .31 | .33 | | | |
| 9,000 CaO | 9 | 1.41 | .30 | .29 | .305±.0061 | .303±.0085 | E |
| | 10 | | .33 | .31 | | | |
| | 11 | | .30 | .33 | | | |
| | 12 | | .29 | .28 | | | |
| 18,000 $CaCO_3$ | 37 | 1.54 | .33 | .35 | .320±.0049 | .310±.0122 | $E_1$ |
| | 38 | | .33 | .30 | | | |
| | 39 | | .32 | .32 | | | |
| | 40 | | .30 | .27 | | | |
| 15,000 CaO | 17 | 2.12 | .34 | .39 | .325±.0073 | .340±.0122 | F |
| | 18 | | .32 | .30 | | | |
| | 19 | | .30 | .34 | | | |
| | 20 | | .34 | .33 | | | |
| 30,000 $CaCO_3$ | 45 | 2.33 | .31 | .27 | .293±.0061 | .273±.0019 | $F_1$ |
| | 46 | | .29 | .27 | | | |
| | 47 | | .30 | .27 | | | |
| | 48 | | .27 | .28 | | | |

TABLE 7. EXPERIMENT 1 — PERCENTAGES OF CALCIUM IN FIRST AND SECOND LAYERS OF SOIL FROM POTS LEACHED WITH DISTILLED WATER FOR ONE YEAR

(Calcium treatments placed in third layer of soil)

| Treatment (pounds per acre) | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|
| | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | Third layer | First layer | Second layer | First layer | Second layer | |
| 15,000 CaO.. | 25 | 2.12 | .32 | .30 | .318±.0066 | .315±.0122 | G |
| | 26 | | .32 | .33 | | | |
| | 27 | | .34 | .35 | | | |
| | 28 | | .29 | .28 | | | |
| 30,000 $CaCO_3$ | 53 | 2.33 | .29 | .35 | .300±.0049 | .313±.0109 | $G_1$ |
| | 54 | | .29 | .32 | | | |
| | 55 | | .31 | .28 | | | |
| | 56 | | .31 | .30 | | | |

TABLE 8. EXPERIMENT 2 — PERCENTAGES OF CALCIUM IN SECOND AND THIRD LAYERS OF SOIL FROM POTS LEACHED WITH DISTILLED WATER FOR ONE YEAR

(Calcium treatments placed in first layer of soil)

| Treatment (pounds per acre) | Fineness of limestone | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|---|
| | | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | | First layer | Second layer | Third layer | Second layer | Third layer | |
| 9,000 $CaCO_3$ | Thru 10-mesh, held on 32-mesh | 57 | 0.91 | .36 | .32 | .328±.0085 | .328 ±.0061 | H |
| | | 58 | | .30 | .33 | | | |
| | | 59 | | .32 | .35 | | | |
| | | 60 | | .33 | .31 | | | |
| 9,000 $CaCO_3$ | Thru 50-mesh, held on 100-mesh | 61 | 0.91 | .28 | .27 | .285±.0049 | .265 ±.0049 | I |
| | | 62 | | .30 | .28 | | | |
| | | 63 | | .29 | .25 | | | |
| | | 64 | | .27 | .26 | | | |
| 9,000 $CaCO_3$ | Thru 200-mesh | 65 | 0.91 | .29 | .28 | .298±.0085 | .295 ±.0061 | J |
| | | 66 | | .32 | .32 | | | |
| | | 67 | | .27 | .29 | | | |
| | | 68 | | .31 | .29 | | | |
| 9,000 $CaCO_3$ | Precipitated $CaCO_3$ | 69 | 0.91 | .33 | .29 | .310±.0146 | .298 ±.0081 | K |
| | | 70 | | .28 | .28 | | | |
| | | 71 | | .35 | .33 | | | |
| | | 72 | | .28 | .29 | | | |

TABLE 9. EXPERIMENT 3 — PERCENTAGES OF CALCIUM IN SECOND AND THIRD LAYERS OF CROPPED AND UNCROPPED SOIL FROM POTS LEACHED WITH DISTILLED WATER FOR FIVE MONTHS

(Calcium treatments placed in first layer of soil)

| Treatment (pounds per acre) | Planted or unplanted | No. of pot | Per cent of calcium in soil layers | | | | | Treatment designation |
|---|---|---|---|---|---|---|---|---|
| | | | Beginning of experiment | End of experiment | | Arithmetic mean | | |
| | | | First layer | Second layer | Third layer | Second layer | Third layer | |
| 3,000 CaO | Planted (oats) | 73 | 0.58 | .21 | .18 | .210±.0073 | .218 ±.0090 | L |
| | | 74 | | .20 | .24 | | | |
| | | 75 | | .19 | .23 | | | |
| | | 76 | | .24 | .22 | | | |
| 3,000 CaO | Unplanted | 77 | 0.58 | .18 | .22 | .195±.0073 | .205 ±.0098 | $L_1$ |
| | | 78 | | .22 | .19 | | | |
| | | 79 | | .20 | .23 | | | |
| | | 80 | | .18 | .18 | | | |

## INTERPRETATION OF ANALYTICAL DATA

The amounts of calcium present in the analyzed layers of soil at the end of the experiments, from the pots that had received the same calcium treatment, varied to some extent, as is seen from tables 5 to 9. The variation in the calcium content of the soil from pots similarly treated appears to be about as great as that shown by a comparison of differently treated pots. In view of this fact, it became necessary to determine the experimental error of the investigation, before any definite conclusions could be drawn regarding the movement of calcium thru the soil, in relation to the following points: (1) Did the analyzed soil layers contain more calcium at the end of the experiments than was contained in the original soils at the beginning of the investigation? (2) Did the layer of soil adjoining the one treated with calcium contain more of this element than the layer farther removed? (3) If calcium had moved thru the soil, did the degree of movement vary with smaller or larger applications of this constituent? In order to draw conclusions accurately from the data presented, the arithmetical mean value with its probable error, for the amount of calcium present in the soil layers resulting from different calcium treatments, was determined. These values are given in the tables and are used in interpreting the results of the investigation For

convenience the letters in the extreme right-hand column of each table are used to designate the different pot treatments.

Peter's formula as given by Mellor (1909) was used in determining the probable errors. According to this formula, the probable error, *R*, of the arithmetical mean of a series of observations is

$$R = \pm 0.8453 \frac{\Sigma (+ v)}{n \sqrt{n-1}}$$

in which $\Sigma (+ v)$ denotes the sum of the deviations of every observation from the mean, their sign being disregarded, and *n* denotes the number of observations actually made. The increase of calcium in one layer of soil over that in another layer, in pots similarly or dissimilarly treated, or the amount of calcium present in the soil from a calcium-treated pot over that in the original soil at the beginning of the experiment, can be determined by subtracting the arithmetical mean value of calcium for any one particular soil from that for any other soil, the probable error of the difference being derived from the formula

$$E = \sqrt{E_1^2 + E_2^2}$$

in which $E_1$ is the probable error of one mean, and $E_2$ the probable error of the other. This procedure is followed in explaining the results of the experiments shown in tables 5 to 9.

A comparison of the amounts of calcium found by analysis in the analyzed soil layers from pots that were similarly treated is given in table 10, which was compiled from the data given in tables 5 to 9 inclusive. This table shows that in eleven cases out of twenty there was a greater amount of calcium in the layer of soil adjoining the one that had been treated with calcium, that in eight of the cases the soil layer farther removed from the treated layer contained the greater percentage of calcium, and that in one case there was an equal amount of calcium in each of the untreated soil layers. The differences in the amounts of calcium in the two soil layers are not great enough to be of any consequence, however. Wood and Stratton (1910) have shown that in order to be significant, differences resulting from different treatments should be at least 3.8 times their probable error, corresponding to odds of 30 to 1 that such differences are real and not due to normal variation. As none of the differences appearing in table 10 are significant, it is safe to con-

clude that the soil layers which were analyzed did not differ in their calcium content for any one particular treatment. This being true, the remainder of the discussion of the results may be confined to a consideration of the soil layer adjacent to the layer receiving the calcium treatment. In every case, regardless of the position of the calcium-treated layers in the pots, this is the second layer of soil.

TABLE 10. COMPARISON OF THE AMOUNTS OF CALCIUM IN THE ANALYZED LAYERS OF SOIL FROM POTS SIMILARLY TREATED

(For the differences to be significant, the mean must be 3.8 times the probable error)

| Treatment | Difference in amounts of calcium | Layer having the greater amount of calcium | Duration of experiment | No. of experiment |
|---|---|---|---|---|
| | In second and third layers | | | |
| A | .020 ± .0109 | Third | | |
| $A_1$ | .020 ± .0147 | Second | Six months | |
| B | .025 ± .0131 | Second | | |
| $B_1$ | .010 ± .0071 | Third | | |
| C | .020 ± .0061 | Second | | |
| $C_1$ | .030 ± .0142 | Third | | |
| D | .005 ± .0156 | Third | | |
| $D_1$ | .010 ± .0149 | Second | | 1 |
| E | .002 ± .0104 | Second | | |
| $E_1$ | .010 ± .0131 | Second | | |
| F | .015 ± .0142 | Third | | |
| $F_1$ | .020 ± .0064 | Second | Twelve months | |
| | In first and second layers | | | |
| G | .003 ± .0138 | First | | |
| $G_1$ | .013 ± .0119 | Second | | |
| | In second and third layers | | | |
| H | .000 ± .0104 | | | |
| I | .020 ± .0069 | Second | Twelve months | 2 |
| J | .003 ± .0104 | Second | | |
| K | .012 ± .0167 | Second | | |
| L | .008 ± .0116 | Third | | |
| $L_1$ | .010 ± .0122 | Third | Five months | 3 |

*Results of experiment 1*

The differences in the percentage of calcium in the second layer of soil, resulting from different calcium treatments, are shown in table 11. It is evident from this table that in the one case when the mean is greater than 3.8 times the probable error, the soil from the pots receiving treat-

TABLE 11. COMPARISON OF THE AMOUNTS OF CALCIUM IN THE SECOND LAYER OF SOIL FROM POTS DIFFERENTLY TREATED IN EXPERIMENT 1

(For the differences to be significant, the mean must be 3.8 times the probable error)

| Treatments compared | Difference in amounts of calcium in second layer of soil | Treatment showing greater amount of calcium | Duration of experiment | Layer of soil in which calcium was placed | Calcium treatments compared |
|---|---|---|---|---|---|
| A and $A_1$ | .055 ± .0156 | A | Six months | First | Equivalent quantities of CaO and $CaCO_3$ |
| B and $B_1$ | .040 ± .0137 | B | | | |
| C and $C_1$ | .075 ± .0088 | C | | | |
| D and $D_1$ | .037 ± .0142 | D | Twelve months | | |
| E and $E_1$ | .015 ± .0078 | $E_1$ | | | |
| F and $F_1$ | .032 ± .0095 | F | | | |
| A and B | .015 ± .0156 | A | Six months | First | Different quantities of CaO |
| A and C | .015 ± .0109 | C | | | |
| B and C | .030 ± .0131 | C | | | |
| D and E | .035 ± .0115 | D | Twelve months | | |
| D and F | .015 ± .0122 | D | | | |
| E and F | .020 ± .0095 | F | | | |
| G and $G_1$ | .002 ± .0163 | G | Twelve months | Third | Equivalent quantities of CaO and $CaCO_3$ |

ment C contained more calcium in the second layer than did the soil from the pots receiving treatment $C_1$. C being greater than $C_1$, and the difference between A and $A_1$ being almost without the experimental error, it appears that the second layer of soil from the pots that were leached for six months contained more calcium when the first layer had been treated with burned limestone than when the first layer had received a treatment of ground limestone. When the soil with similar treatments

was leached for twelve months, this relationship between the burned and the ground limestone treatments is not shown, as can be seen from the table. It seems reasonable to believe that the results from the soil that was leached for the longer period are nearer the truth, as this soil had a longer time in which to become adjusted to the conditions of the experiment. If this assumption is true, it can be concluded from the results given in table 11 that the burned limestone did not move downward in the soil more rapidly than did the ground limestone. The table also reveals the fact that there was no more calcium present in the second layer of soil resulting from larger applications of burned limestone than there was from smaller applications of this substance, and that there was no appreciable difference between the amounts of calcium present in the second layer of soil from the pots that had been treated with either burned limestone or ground limestone in the third layer.

The question now arising is whether or not the amounts of calcium present in the second layer of soil from the pots in experiment 1 which were treated with burned limestone (since the tendency was for the pots treated with burned limestone to contain more calcium in the second soil layer than those treated with ground limestone) are large enough, when compared with the amount of calcium in the soil at the beginning

TABLE 12. COMPARISON OF THE AMOUNTS OF CALCIUM FOUND IN THE SECOND LAYER OF SOIL AT THE END OF EXPERIMENT 1, WITH THE AMOUNT PRESENT IN THE SOIL AT THE BEGINNING OF THE EXPERIMENT

(For the differences to be significant, the mean must be 3.8 times the probable error)

| Treatment | Calcium present in second layer of soil at end of experiment | Calcium present in soil at beginning of experiment | Difference in calcium | Duration of experiment |
|---|---|---|---|---|
| A | .370 ± .0098 | .328 ± .0156 | .042 ± .0184 | Six months |
| B | .355 ± .0122 | | .027 ± .0198 | |
| C | .385 ± .0049 | | .057 ± .0164 | |
| D | .340 ± .0098 | .328 ± .0156 | .012 ± .0184 | Twelve months |
| E | .305 ± .0061 | | .023 ± .0168 | |
| F | .325 ± .0073 | | .003 ± .0172 | |
| G | .318 ± .0066 | | .010 ± .0169 | |

of the experiment, to show that there was an upward or a downward movement of this constituent during the course of the experiment. Such a comparison is made in table 12. Treatment C shows a downward, movement of calcium into the second soil layer that is almost within certainty; but since treatments A, B, D, E, and F do not indicate such a movement, it can be concluded that there has been no downward movement of calcium within the soil. No upward movement of calcium resulted from treatment G, as can be seen from the table.

*Results of experiments 2 and 3*

The results of experiments 2 and 3 are interpreted in the same way as are those of experiment 1, and are summarized in tables 13 and 14:

TABLE 13. COMPARISON OF THE AMOUNTS OF CALCIUM FOUND IN THE SECOND LAYER OF SOIL AT THE END OF EXPERIMENT 2, WITH THE AMOUNT PRESENT IN THE SOIL AT THE BEGINNING OF THE EXPERIMENT

(Limestone added in equal amounts. For the differences to be significant, the mean must be 3.8 times the probable error)

| Treatment | Calcium present in second layer of soil at end of experiment | Calcium present in soil at beginning of experiment | Difference in calcium | Duration of experiment | Layer of soil in which calcium was placed | Fineness of limestone applied |
|---|---|---|---|---|---|---|
| H | .328 ±.0085 | .300 ±.0154 | .028 ±.0176 | Twelve months | First | H—Thru 10-mesh sieve, held on 32-mesh |
| I | .285 ±.0049 | | .015 ±.0162 | | | I—Thru 50-mesh sieve, held on 100-mesh |
| J | .298 ±.0085 | | .002 ±.0176 | | | J—Thru 200-mesh sieve |
| K | .310 ±.0146 | | .010 ±.0212 | | | K—Precipitated $CaCO_3$ |

There was no movement of calcium from the first to the second layer of soil in the pots that were treated with ground limestone at the rate of 9000 pounds to the acre, regardless of the fineness to which the limestone had been ground, nor with an equivalent quantity of precipitated calcium carbonate. This fact is well brought out by the figures in table 13. The differences shown in the table between the amount of calcium in the soil at the beginning of the experiment and that found in the second soil layer at the end of the experiment are not great enough to indicate any movement of this element.

In table 14 it is shown clearly that growing oats on the potted soil treated with burned limestone at the rate of 3000 pounds to the acre had no influence on the downward movement of calcium thru the soil. There was no movement of calcium in the soil either with or without the growth

TABLE 14. COMPARISON OF THE AMOUNTS OF CALCIUM IN THE SECOND LAYER OF SOIL FROM PLANTED AND UNPLANTED POTS IN EXPERIMENT 3

(Calcium added in equal amounts as burned limestone. For the differences to be significant, the mean must be 3.8 times the probable error)

| Treatments compared | Difference in amounts of calcium in second layer of soil | Treatment showing greater amount of calcium | Duration of experiment | Layer of soil in which calcium was placed |
|---|---|---|---|---|
| L and $L_1$ | .015 ± .0103 | L | Five months | First |
| L and Z* | .010 ± .0088 | Z | | |

*Z (original soil) = .220 ± .0049

of plants, as is shown by a comparison of the calcium present in the second soil layer at the end of the experiment with that present in the soil at the time when the experiment was begun.

## SUMMARY

Calcium applied to a clayey silt loam soil in the form of burned limestone, ground limestone, or precipitated calcium carbonate, did not move downward in the soil to any appreciable extent when the soil was leached in pots for one year with distilled water.

The soil from some of the pots that were leached for six months showed a slight movement of calcium when the soil had been treated with burned limestone, while the soil from the pots leached for twelve months with similar treatments did not show such a movement. This inconsistency cannot be explained unless there was a mechanical movement of calcium in the soil from certain of the pots that were leached for six months. As hereinbefore stated, the results obtained from the soil leached for the longer period are given preference over the others, and this permits

the conclusion that neither small nor large applications of burned or ground limestone resulted in a downward movement of calcium.

Calcium incorporated with the soil as burned or ground limestone and placed in the bottom of the pots did not move by diffusion into the upper soil layers.

No movement of ground limestone thru the soil was evident when applied at the rate of 9000 pounds to the acre, irrespective of the fineness to which the rock had been ground. There was no difference in the movement of limestone ground to pass a 200-mesh sieve and that held on a 32-mesh sieve.

Precipitated calcium carbonate when applied to the soil in large amounts did not move downward to the untreated adjacent soil.

Oats grown in pots on the soil that had been treated with burned limestone had no effect in bringing about a descent of calcium.

It seems logical to believe that a soil deficient in calcium will absorb this constituent from the drainage water as it percolates thru the soil. No doubt this occurs, but the amount held by the soil is evidently so small that it cannot be detected by a chemical analysis. Conclusions drawn from small differences of calcium found in soil upon analysis are hardly trustworthy, as it is often difficult to obtain concordant results from the same sample of soil. When small differences are calculated to pounds of calcium in an acre foot of soil, as is often done, the real value of such results is questionable.

## CONCLUSION

The results of this investigation are summarized briefly in the following statement:

The translocation of calcium thru a clayey silt loam soil with a rather large lime requirement is extremely slow, since in these experiments no upward nor downward movement of this element was perceptible twelve months after small, large, or excessive amounts of calcium salts were applied to the soil.

## ACKNOWLEDGMENT

The writer desires to acknowledge his indebtedness to Professor T. Lyttleton Lyon, under whose direction this work was done

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CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

# A STUDY OF BACTERIA IN ICE CREAM DURING STORAGE

H. B. ELLENBERGER

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# A STUDY OF BACTERIA IN ICE CREAM DURING STORAGE

# A STUDY OF BACTERIA IN ICE CREAM DURING STORAGE

H. B. Ellenberger

Within very recent years ice cream has passed from a luxury, only occasionally indulged in, to one of the commonest of desserts and confections. The annual consumption of ice cream in the United States amounts to almost two gallons per capita, and consumers last year paid nearly three hundred million dollars to indulge their appetite for this popular dish.

Because of the size and the rapid growth of the industry, ice cream has drawn the attention of the food expert and the health officer. Other dairy products are forced to conform to certain arbitrary standards of composition and bacteria content, and ice cream is being given a great deal of attention in this respect. A few cities have already passed bacterial standards, and many more are studying the situation and would act if they were sure they could make an equitable ruling. To add to the knowledge of the subject, and in the hope of obtaining information applicable to the industry, certain studies have been undertaken by the writer to determine the influence of some of the more important factors on the bacteria content of ice cream, and particularly the effect of storage on the total number and the classes of bacteria found. Certain practices of plating, and the use of different media and different incubation temperatures, were studied in their relation to the bacterial analysis of ice cream.

## PLAN OF WORK

The various experimental batches of ice cream were frozen in a ten-gallon brine freezer. Enough cream, direct from the separator, was obtained at one time to make up five ten-gallon mixes. The milk from which this cream was separated was received at one of the college skimming stations, about fifteen miles away, cooled, shipped in to the College on the following day, and separated. Bulk condensed milk, shipped direct from a condensery, was used in the groups of samples designated A and B, while those designated C and D contained only cream, sugar, vanilla, and gelatin.

All utensils used, except the freezer, were sterilized with live steam for several hours shortly before using. The freezer was steamed thoroly

from a steam hose just before the various batches were frozen. Checks on its sterility were obtained by passing one-half liter of sterile water thru the freezer while it was in motion, and then plating samples of this water.

As soon as it was received from the separator, the cream was cooled, standardized, and divided into five batches, as follows:

No. 1 was mixed and frozen at once.

No. 2 was held for one day, and was then mixed and frozen. No platings were made from this batch. It was frozen in order to determine the influence of aging the cream on the swell.

No. 3 was held for two days, and was then mixed and frozen.

No. 4 was pasteurized at 145° F. for thirty minutes, cooled, held for two days, and then mixed and frozen.

No. 5 was mixed ready for freezing, except for the gelatin and the flavoring, pasteurized at 145° F. for thirty minutes, cooled, and held for two days, after which the gelatin and the flavoring were added and the mixture was frozen.

The temperature at which the batches were held was maintained at near 32° F.

After freezing, one packing can of ice cream from each batch was placed in an artificially cooled hardening room, where it was kept frozen at a temperature of from 10° to 15° F. Thus it was easily accessible for sampling. Samples for plating were taken from each of the ingredients entering the mix, from the mix itself, and from the freshly frozen ice cream. After hardening, the ice cream in each can was sampled and plated on the second, fourth, sixth, eighth, eleventh, fourteenth, seventeenth, twenty-first, twenty-fifth, twenty-ninth, forty-fifth, sixtieth, seventy-fifth, ninetieth, and one hundred and twentieth days.

Platings were made on lactose agar and on litmus lactose gelatin, by which the colonies were divided into acid-forming, inert, and liquefying groups. To further differentiate between the different groups of bacteria according to their action on milk, colonies were picked from agar plates and inoculated into tubes of sterile litmus milk. These milk tubes were then incubated at 37° C. for ten days, and the reaction produced in the milk was recorded on the second, fifth, and tenth days, thereby dividing the bacteria into groups of acid-coagulating, acid-forming, inert, alkali-forming, and peptonizing.

All plates were incubated at 20° C. and counted on the seventh day, except in the case of certain gelatin plates containing rapid liquefiers which had to be counted in a shorter time.

The gelatin was made up as follows: gelatin 15 per cent, peptone 1 per cent, beef extract 0.5 per cent, lactose 1 per cent. It was titrated to an acidity of +10, Fuller's scale.

The composition of the lactose agar used was: thread agar 1.5 per cent, peptone 1 per cent, beef extract 0.5 per cent, lactose 1 per cent. This was titrated to +10 acidity, Fuller's scale.

### Methods of sampling for bacteria tests

Thruout these studies, all samples for plating were taken in a uniform manner by first removing the surface of the ice cream to a depth of one-half inch with a sterile spoon, and then removing a sample with a sterile butter trier. The sample was transferred to an ordinary dilution bottle and allowed to melt at room temperature, after which it was thoroly mixed by shaking, and about one cubic centimeter was transferred with a sterile pipette to a weighing bottle and weighed. Dilutions were all calculated from the weight; therefore the counts of bacteria are expressed in the number per gram, not in the number per cubic centimeter.

### Sources of bacteria in ice cream

Since the larger part of the ice-cream mix is composed of cream or of milk and cream, it is natural to suppose that the bacteria content of freshly frozen ice cream is largely determined by the number of bacteria present in these materials. This is substantiated by Hammer (1912)[1] and by Bahlman (1914). It is of interest to note the numbers of bacteria present in each of the ingredients as they entered the various mixes thruout these trials, which were as follows:

| | Minimum number of bacteria | Maximum number of bacteria |
|---|---|---|
| Standardized cream | 1,150 | 37,600,000 |
| Condensed milk | 31,500 | 59,800,000 |
| Sugar | 20 | 255 |
| Gelatin | 48 | 891 |
| Flavoring | 10 | 321 |

[1] Dates in parenthesis refer to Bibliography, page 362

In order to make sure that the freezer did not contaminate the ice cream, 500 cubic centimeters of sterile water was run thru it, as previously noted. Samples of this water when plated gave counts varying from 10 to 55 bacteria per cubic centimeter, with an average of 28.

From these figures it is readily seen that the cream and the condensed milk supplied most of the bacteria which entered the ice cream.

### EFFECT OF FREEZING PROCESS ON NUMBER OF BACTERIA

In spite of the fact that, as has been shown, the number of bacteria in the freezer was negligible as a factor in increasing the bacteria count of the ice cream, yet in almost every case the fresh ice cream, as it came from the freezer, gave much higher counts than did the mix as it entered the freezer. An average increase of 48 per cent is shown in table 1 (page 336). Gordon (Gordon, Prescott, Heinemann, and Pease, 1914) obtained similar results. This may perhaps be accounted for in the breaking-up of clumps of bacteria by the beating received from the dasher during freezing. It is possible that thru freezing these clumps are rendered brittle, which would cause them to break apart more readily.

### TOTAL NUMBERS OF BACTERIA IN ICE CREAM DURING STORAGE

Stiles (Stiles and Pennington, 1909:263–265) made counts at various intervals of the total numbers of bacteria in four samples of ice cream which he held frozen hard for a period of thirty-four days. These samples showed rather wide variations, but in general the number of bacteria increased up to the third day of storage, after which there was a gradual decrease to the fourteenth day. There was then a more rapid increase, until the highest counts were reached on the twenty-seventh day. On the thirty-fourth day the counts were about equal to those of the fourteenth day. These samples were purchased from retailers and their age at the time of purchase was not stated. Pennington (Stiles and Pennington, 1909:266–269) held eight samples of ice cream for periods of from three to ten days. The counts during these storage periods showed wide variations, but for the most part there was more or less decrease during the first twenty-four hours. The history of these samples before purchase was unknown.

Hammer (1912) stored twelve samples of ice cream for periods of from three to forty-four days. He concludes that the number of bacteria developing on agar at 37° C. does not increase during storage if the product

is kept suitably hardened. Esten and Mason (1915) concluded, after holding several samples of ice cream for about a month, that " when ice cream is kept frozen for periods of at least a month there is no marked increase or decrease in the bacterial content as shown by litmus lactose gelatin plate cultures. The percentage of acid bacteria and of liquefying bacteria also remained fairly constant."

The average counts of the fourteen samples in the trials described in this paper, made at various times during the storage period of one hundred

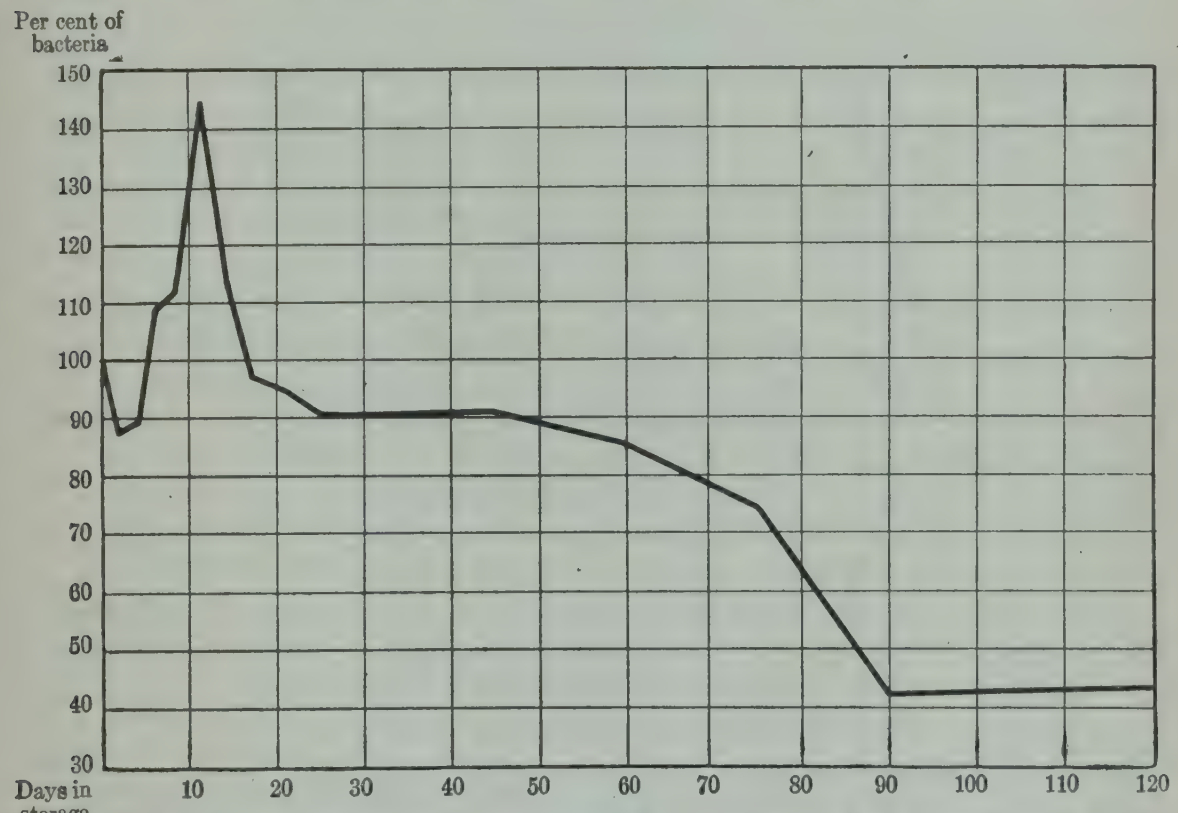


Fig. 75. Average percentage increase and decrease of bacteria in fourteen samples of ice cream during a storage period of 120 days

and twenty days and reported in table 1, indicate a slight decrease in total numbers during the first four days of storage, with a noticeable increase from the fourth to the eighth day, after which there is a gradual decline until the end of the period.

The percentage increase or decrease in numbers of bacteria in each sample during the storage period, and also the average percentage variation on all samples, are shown in table 2. The latter is also charted by curve in figure 75. All percentages are calculated from the count of the freshly frozen ice cream. This shows a drop to 89.1 per cent of the initial

TABLE 1. TOTAL NUMBERS OF BACTERIA PER GRAM IN THE MIX, IN THE FRESHLY FROZEN ICE CREAM, AND IN THE ICE CREAM AT VARIOUS PERIODS DURING STORAGE, AS SHOWN BY LACTOSE AGAR PLATES INCUBATED AT 20° C.

| Sample | A 1 | A 3 | A 4 | A 5 | B 1 | B 3 | B 4 | B 5 | C 3 | C 4 | C 5 | D 3 | D 4 | D 5 | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mix | 7,065,000 | 10,500,000 | 5,990,000 | 500 | 18,240,000 | 25,850,000 | 39,900 | 25,200 | 20,400,000 | 107,600 | 176,400 | 3,700,000 | 6,900 | 7,950 | 6,579,246 |
| Frozen | 6,600,000 | 11,900,000 | 6,380,000 | 1,500 | 25,280,000 | 50,400,000 | 88,100 | 45,000 | 31,100,000 | 873,200 | 499,200 | 3,100,000 | 26,000 | 21,500 | 9,736,750 |
| 2d day | 6,830,000 | 9,350,000 | 7,104,000 | 1,250 | 25,600,000 | 30,400,000 | 29,650 | 39,000 | 50,732,000 | 432,000 | 320,000 | 3,400,000 | 16,600 | 25,500 | 9,591,428 |
| 4th day | 7,720,000 | 13,400,000 | 6,780,000 | 1,150 | 28,900,000 | 43,900,000 | 80,000 | 42,850 | 26,200,000 | 375,500 | 365,700 | 3,000,000 | 16,100 | 18,900 | 9,342,871 |
| 6th day | 8,550,000 | 11,200,000 | 6,300,000 | 2,100 | 37,600,000 | 47,500,000 | 56,500 | 48,000 | 22,266,600 | 1,050,000 | 1,002,000 | 3,550,000 | 18,800 | 15,750 | 9,939,982 |
| 8th day | 7,650,000 | 16,333,000 | 8,050,000 | 1,800 | 42,000,000 | 44,800,000 | 56,000 | 37,000 | 25,600,000 | 995,000 | 995,000 | 3,550,000 | 17,900 | 18,200 | 10,721,707 |
| 11th day | 9,500,000 | 14,800,000 | 8,250,000 | 2,600 | 28,000,000 | 49,100,000 | 48,500 | 32,350 | 27,200,000 | 2,700,000 | 2,270,000 | 3,150,000 | 18,600 | 19,850 | 10,363,707 |
| 14th day | 8,150,000 | 13,000,000 | 8,600,000 | 3,150 | 33,600,000 | 37,000,000 | 50,000 | 47,500 | 31,500,000 | 1,020,000 | 830,000 | 3,300,000 | 19,300 | 17,500 | 9,795,532 |
| 17th day | 7,350,000 | 13,250,000 | 8,400,000 | 1,750 | 31,800,000 | 43,500,000 | 49,000 | 44,000 | 21,600,000 | 775,000 | 736,660 | 2,033,300 | 13,840 | 21,000 | 9,255,325 |
| 21st day | 8,700,000 | 12,800,000 | 6,900,000 | 1,850 | 31,600,000 | 44,400,000 | 51,500 | 54,500 | 26,000,000 | 570,000 | 565,000 | 1,975,000 | 16,000 | 16,050 | 9,546,421 |
| 25th day | 7,300,000 | 12,300,000 | 6,250,000 | 1,400 | 52,600,000 | 33,000,000 | 58,000 | 39,500 | 18,000,000 | 673,300 | 652,500 | 1,575,000 | 15,450 | 13,350 | 9,462,750 |
| 29th day | 7,600,000 | 13,500,000 | 7,750,000 | 1,650 | 38,500,000 | 34,000,000 | 46,000 | 40,000 | 23,200,000 | 363,300 | 446,600 | 3,187,500 | 13,300 | 18,400 | 9,190,482 |
| 45th day | 2,800,000 | 12,200,000 | 6,500,000 | 2,500 | 25,000,000 | 36,750,000 | 47,300 | 40,500 | 23,650,000 | 857,500 | 830,000 | 2,475,000 | 12,500 | 16,600 | 7,941,564 |
| 60th day | 4,700,000 | 9,800,000 | 6,600,000 | 1,175 | 32,400,000 | 28,750,000 | 48,750 | 41,250 | 16,800,000 | 695,000 | 960,000 | 2,150,000 | 16,660 | 14,850 | 7,355,549 |
| 75th day | 4,625,000 | 10,850,000 | 6,500,000 | 1,210 | 22,600,000 | 31,500,000 | 53,250 | 36,750 | 10,400,000 | 696,600 | 813,300 | 1,112,500 | 11,100 | 10,500 | 6,372,158 |
| 90th day | 1,800,000 | 1,500,000 | 5,550,000 | 633 | 15,866,600 | 25,333,300 | 30,500 | 32,000 | 10,000,000 | 65,000 | 44,000 | 1,593,750 | 14,650 | 11,866 | 4,417,307 |
| 120th day | 2,737,500 | 5,525,000 | 5,875,000 | 490 | 7,200,000 | 9,700,000 | 32,625 | 22,500 | 7,966,600 | 172,500 | 259,000 | 1,810,000 | 14,600 | 11,270 | 2,951,935 |

TABLE 2. Variation in Bacterial Counts, Expressed in Percentage of the Count of the Freshly Frozen Ice Cream

| Sample | A 1 | A 3 | A 4 | A 5 | B 1 | B 3 | B 4 | B 5 | C 3 | C 4 | C 5 | D 3 | D 4 | D 5 | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Frozen | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 2d day | 103.5 | 78.6 | 111.3 | 85.3 | 101.3 | 60.3 | 33.6 | 86.7 | 163.1 | 49.5 | 64.1 | 109.7 | 63.8 | 118.6 | 87.7 |
| 4th day | 117.0 | 112.6 | 106.3 | 76.7 | 114.3 | 87.1 | 90.8 | 95.2 | 84.2 | 43.0 | 73.2 | 96.8 | 61.9 | 87.9 | 89.1 |
| 6th day | 129.5 | 94.1 | 98.7 | 140.0 | 148.7 | 94.2 | 64.1 | 106.7 | 71.6 | 120.2 | 200.7 | 114.5 | 72.3 | 73.2 | 109.2 |
| 8th day | 115.9 | 137.2 | 126.2 | 120.0 | 166.1 | 88.9 | 63.6 | 82.2 | 82.3 | 113.9 | 199.3 | 114.5 | 68.8 | 84.6 | 111.7 |
| 11th day | 143.9 | 124.4 | 129.3 | 173.3 | 110.7 | 97.4 | 55.0 | 71.9 | 87.4 | 309.2 | 454.7 | 101.6 | 71.5 | 92.3 | 144.5 |
| 14th day | 123.5 | 109.2 | 134.8 | 210.0 | 132.9 | 73.4 | 56.7 | 105.5 | 101.3 | 116.8 | 166.3 | 106.4 | 74.2 | 81.4 | 113.7 |
| 17th day | 111.4 | 111.3 | 131.7 | 116.7 | 125.8 | 86.3 | 55.6 | 97.8 | 69.4 | 88.7 | 147.6 | 65.6 | 53.2 | 97.7 | 97.1 |
| 21st day | 131.8 | 107.6 | 108.1 | 123.3 | 125.0 | 88.1 | 58.4 | 121.1 | 83.6 | 65.3 | 113.2 | 63.7 | 61.5 | 74.6 | 94.7 |
| 25th day | 110.6 | 103.4 | 98.0 | 93.3 | 208.1 | 65.5 | 65.8 | 87.8 | 57.9 | 77.1 | 130.7 | 50.8 | 59.4 | 62.1 | 90.8 |
| 29th day | 115.1 | 113.4 | 121.5 | 110.0 | 152.3 | 67.5 | 52.2 | 88.9 | 74.6 | 41.6 | 89.5 | 102.8 | 51.1 | 85.6 | 90.4 |
| 45th day | 42.4 | 102.5 | 101.9 | 166.7 | 98.9 | 72.9 | 53.7 | 90.0 | 76.0 | 98.2 | 166.3 | 79.8 | 48.1 | 77.2 | 91.0 |
| 60th day | 71.2 | 82.3 | 103.4 | 78.3 | 128.2 | 57.0 | 55.3 | 91.7 | 54.0 | 79.6 | 192.3 | 69.3 | 64.1 | 69.1 | 85.4 |
| 75th day | 70.1 | 91.2 | 101.9 | 80.7 | 89.4 | 62.5 | 60.4 | 81.7 | 33.4 | 79.8 | 162.9 | 35.9 | 42.7 | 48.8 | 74.4 |
| 90th day | 27.3 | 12.6 | 87.0 | 42.2 | 62.8 | 50.3 | 34.6 | 71.1 | 32.1 | 7.4 | 8.8 | 51.4 | 56.3 | 55.2 | 42.8 |
| 120th day | 41.5 | 46.4 | 92.1 | 32.7 | 28.5 | 19.2 | 37.0 | 50.0 | 25.6 | 19.7 | 51.9 | 58.4 | 56.1 | 52.4 | 43.7 |

count during the first four days of storage, after which there is a rapid increase to 144.5 per cent reached on the eleventh day, then just as rapid a drop back to 97.1 per cent on the seventeenth day, followed by a less noticeable gradual decrease to about 43 per cent at the ninetieth- and one-hundred-and-twentieth-day periods.

## GROUPS OF BACTERIA FOUND DURING STORAGE

### *Groups shown by litmus gelatin plates*

For a quick method of dividing the bacteria into groups, the litmus lactose gelatin plates were used. From these plates the colonies developing can be divided into three groups — acid-forming, inert, and liquefying. This method of grouping was used on samples of each mix and on the ice cream samples, which were plated on the eighth, seventeenth, twenty-ninth, forty-fifth, sixtieth, seventy-fifth, and ninetieth days of storage. The results obtained from each of the fourteen samples, expressed in percentage of the total count, are given in table 3. The average of these one hundred and five trials shows that 80.2 per cent of the total number of bacteria were acid formers, 14.9 per cent were inert, and 4.9 per cent were liquefiers. The acid-forming group shows a tendency to increase from the mix to the twenty-ninth day of storage, while the inert group shows a corresponding decrease. After the twenty-ninth day the acid formers show a decrease, while both the inert and the liquefying group show some increase.

A comparison of the groups developing from ice cream made of raw cream, with those in ice cream made of pasteurized cream, is shown in table 4. Sample 3 in each of the four trials was made from raw cream, while samples 4 and 5 were made from the same cream pasteurized. The pasteurized samples show a lower proportion of acid-forming bacteria thruout, but a higher proportion of the inert and liquefying groups.

### *Groups shown by litmus milk tubes*

While nearly all of the acid-forming groups found on litmus gelatin plates produce acid in milk, the action on milk of the other two classes of bacteria, inert and liquefying, is very doubtful. Even among the acid-forming groups there are found subgroups of organisms showing very different action on milk; some of these cause coagulation, others do not,

TABLE 3. PERCENTAGES OF BACTERIA IN VARIOUS GROUPS AS SHOWN BY LITMUS LACTOSE GELATIN PLATES

| Sample | A 1 | | | A 3 | | | A 4 | | | A 5 | | | B 1 | | | B 3 | | | B 4 | | | B 5 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying |
| Mix | 0.8 | 85.3 | 13.9 | 87.5 | 6.3 | 6.2 | 66.1 | 30.3 | 3.6 | ..... | ..... | ..... | 85.3 | 13.2 | 1.5 | 87.9 | 9.1 | 3.0 | 64.8 | 31.0 | 4.2 | 70.0 | 20.0 | 10.0 |
| 8th day | 80.0 | 16.0 | 4.0 | 79.5 | 11.7 | 8.8 | 90.0 | 10.0 | 0.0 | 77.7 | 22.3 | 0.0 | 96.2 | 1.3 | 2.5 | 90.0 | 3.4 | 6.6 | 55.0 | 45.0 | 0.0 | 85.7 | 14.3 | 0.0 |
| 17th day | 50.0 | 25.0 | 25.0 | 100.0 | 0.0 | 0.0 | 70.0 | 20.0 | 10.0 | 93.3 | 2.8 | 3.9 | 93.6 | 6.4 | 0.0 | 100.0 | 0.0 | 0.0 | 80.0 | 20.0 | 0.0 | 100.0 | 0.0 | 0.0 |
| 29th day | 76.4 | 11.9 | 11.7 | 89.4 | 8.0 | 2.6 | 81.8 | 18.2 | 0.0 | 94.6 | 2.4 | 3.0 | 98.0 | 1.0 | 1.0 | 91.7 | 0.0 | 8.3 | 92.1 | 6.8 | 1.1 | 93.1 | 6.9 | 0.0 |
| 45th day | 87.5 | 0.0 | 12.5 | 76.9 | 23.1 | 0.0 | 82.4 | 17.6 | 0.0 | 62.5 | 12.5 | 25.0 | 92.9 | 7.1 | 0.0 | 82.7 | 13.9 | 3.4 | 75.0 | 18.8 | 6.2 | 76.9 | 8.0 | 15.1 |
| 60th day | 91.6 | 4.3 | 4.1 | 95.5 | 0.0 | 4.5 | 60.0 | 13.3 | 26.7 | 80.3 | 16.7 | 3.0 | 82.1 | 17.9 | 0.0 | 98.3 | 1.7 | 0.0 | 95.4 | 4.6 | 0.0 | 83.3 | 16.7 | 0.0 |
| 75th day | 87.5 | 12.5 | 0.0 | 80.0 | 15.0 | 5.0 | 88.8 | 11.2 | 0.0 | 60.7 | 37.7 | 1.6 | 96.2 | 2.6 | 1.2 | 92.0 | 6.0 | 2.0 | 88.8 | 11.2 | 0.0 | 77.0 | 19.2 | 3.8 |
| 90th day | 81.2 | 12.6 | 6.2 | 82.6 | 17.4 | 0.0 | 90.9 | 0.0 | 9.1 | 67.5 | 25.7 | 6.8 | 84.1 | 14.3 | 1.6 | 79.2 | 12.5 | 8.3 | 78.1 | 12.8 | 9.1 | 69.2 | 19.3 | 11.5 |
| Average | 69.4 | 20.9 | 9.7 | 86.4 | 10.2 | 3.4 | 78.7 | 15.1 | 6.2 | 76.7 | 17.1 | 6.2 | 91.0 | 8.0 | 1.0 | 90.2 | 5.8 | 4.0 | 78.6 | 18.8 | 2.6 | 81.9 | 13.1 | 5.0 |

| Sample | C 3 | | | C 4 | | | C 5 | | | D 3 | | | D 4 | | | D 5 | | | Average of all samples | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefyin |
| Mix | 97.6 | 0.0 | 2.4 | 67.3 | 30.7 | 2.0 | 85.8 | 14.2 | 0.0 | 79.0 | 9.4 | 11.6 | 75.0 | 12.5 | 12.5 | 80.0 | 15.0 | 5.0 | 72.9 | 21.3 | 5.8 |
| 8th day | 89.7 | 7.8 | 2.5 | 85.6 | 14.4 | 0.0 | 78.2 | 21.8 | 0.0 | 92.3 | 5.1 | 2.6 | 82.5 | 17.5 | 0.0 | 63.6 | 36.4 | 0.0 | 81.9 | 16.2 | 1.9 |
| 17th day | ..... | ..... | ..... | 80.0 | 0.0 | 20.0 | 84.2 | 10.6 | 5.2 | 94.5 | 3.7 | 1.8 | 93.8 | 6.2 | 0.0 | 95.6 | 2.2 | 2.2 | 87.3 | 7.5 | 5.2 |
| 29th day | 95.5 | 3.4 | 1.1 | 80.0 | 20.0 | 0.0 | 85.0 | 15.0 | 0.0 | 97.1 | 1.0 | 1.9 | 95.1 | 4.9 | 0.0 | 93.9 | 6.1 | 0.0 | 90.3 | 7.5 | 2.2 |
| 45th day | ..... | ..... | ..... | 90.4 | 9.6 | 0.0 | 80.0 | 20.0 | 0.0 | 94.8 | 3.9 | 1.3 | 97.4 | 1.7 | 0.9 | 4.9 | 91.5 | 3.6 | 77.3 | 17.5 | 5.2 |
| 60th day | 90.0 | 9.2 | 0.8 | 66.7 | 33.3 | 0.0 | 60.0 | 40.0 | 0.0 | 92.0 | 8.0 | 0.0 | 65.6 | 34.4 | 0.0 | 81.4 | 18.6 | 0.0 | 81.6 | 15.6 | 2.8 |
| 75th day | 73.0 | 21.6 | 5.4 | 66.7 | 0.0 | 33.3 | 40.0 | 30.0 | 30.0 | 72.2 | 22.3 | 5.5 | ..... | ..... | ..... | 45.6 | 26.4 | 28.0 | 74.5 | 16.6 | 8.9 |
| 90th day | 71.0 | 18.8 | 10.2 | 59.1 | 27.3 | 13.6 | ..... | ..... | ..... | 53.9 | 30.7 | 15.4 | ..... | ..... | ..... | ..... | ..... | ..... | 74.3 | 17.4 | 8.3 |
| Average | 86.1 | 10.1 | 3.8 | 74.5 | 16.9 | 8.6 | 73.3 | 21.7 | 5.0 | 84.5 | 10.5 | 5.0 | 84.9 | 12.9 | 2.2 | 66.4 | 28.0 | 5.6 | 80.2 | 14.9 | 4.9 |

TABLE 4. PERCENTAGES OF BACTERIA IN VARIOUS GROUPS AS SHOWN ON LITMUS LACTOSE GELATIN, FROM ICE CREAM MADE OF RAW AND OF PASTEURIZED CREAM

| Sample | Raw cream | | | Pasteurized cream | | |
|---|---|---|---|---|---|---|
| | Acid-forming | Inert | Liquefying | Acid-forming | Inert | Liquefying |
| A 3 | 86.4 | 10.2 | 3.4 | ..... | ..... | ..... |
| A 4 | ..... | ..... | ..... | 78.7 | 15.1 | 6.2 |
| A 5 | ..... | ..... | ..... | 76.7 | 17.1 | 6.2 |
| B 3 | 90.2 | 5.8 | 4.0 | ..... | ..... | ..... |
| B 4 | ..... | ..... | ..... | 78.6 | 18.8 | 2.6 |
| B 5 | ..... | ..... | ..... | 81.9 | 13.1 | 5.0 |
| C 3 | 86.1 | 10.1 | 3.8 | ..... | ..... | ..... |
| C 4 | ..... | ..... | ..... | 74.5 | 16.9 | 8.6 |
| C 5 | ..... | ..... | ..... | 73.3 | 21.7 | 5.0 |
| D 3 | 84.5 | 10.5 | 5.0 | ..... | ..... | ..... |
| D 4 | ..... | ..... | ..... | 84.9 | 12.9 | 2.2 |
| D 5 | ..... | ..... | ..... | 66.4 | 28.0 | 5.6 |
| Average | 86.8 | 9.2 | 4.0 | 76.9 | 17.9 | 5.2 |

and still others ferment the milk sugar, forming gas. To divide the organisms into groups according to the action shown on milk, the milk-tube method, previously mentioned, was used. By this means Ayers and Johnson (1915) obtained the following average from 71 samples of commercial ice cream tested during the summer in Washington, D. C.:

| | Per cent |
|---|---|
| Acid-coagulating | 49.82 |
| Acid-forming | 20.72 |
| Inert | 13.98 |
| Alkali-forming | 1.86 |
| Peptonizing | 13.62 |

In the writer's experiments, groups were determined by the milk-tube method from the same samples as were used with the gelatin plates. Individual colonies were picked from a representative agar plate and inoculated into tubes of litmus milk, which were incubated at 37° C. On the basis of the ten-day reaction in this litmus milk, the bacteria were divided into five groups — acid-coagulating, acid-forming, inert, alkali-forming, and peptonizing. The results, expressed in percentages of the total count, are summarized in table 5. The average of these one hundred

TABLE 5. Percentages of Bacteria in Various Groups as Shown by Litmus Milk Tubes

| Sample | A 1 | | | | A 3 | | | | A 4 | | | | A 5 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming |
| Mix | 29.4 | 5.9 | 54.9 | 7.8 | 16.7 | 9.5 | 71.4 | 0 | 39.6 | 54.7 | 3.8 | 0 | 40.0 | 0.0 | 60.0 | 0 |
| 8th day | 46.2 | 11.5 | 42.3 | 0.0 | 28.6 | 14.3 | 57.1 | 0 | 23.3 | 2.1 | 72.5 | 0 | 48.0 | 24.0 | 24.0 | 0 |
| 17th day | 48.7 | 10.2 | 38.5 | 0.0 | 44.9 | 6.1 | 49.0 | 0 | 27.9 | 9.3 | 62.8 | 0 | 78.6 | 14.3 | 7.1 | 0 |
| 29th day | 51.3 | 5.1 | 43.6 | 0.0 | 22.4 | 4.1 | 73.5 | 0 | 26.1 | 0.0 | 73.9 | 0 | 62.9 | 34.3 | 2.8 | 0 |
| 45th day | 40.0 | 4.0 | 56.0 | 0.0 | 32.4 | 14.7 | 52.9 | 0 | 29.0 | 6.5 | 64.5 | 0 | 78.3 | 13.0 | 8.7 | 0 |
| 60th day | 30.0 | 5.0 | 65.0 | 0.0 | 31.1 | 11.1 | 57.8 | 0 | 7.8 | 5.9 | 86.3 | 0 | 83.8 | 5.4 | 5.4 | 0 |
| 75th day | 41.0 | 7.7 | 51.3 | 0.0 | 29.0 | 10.5 | 60.5 | 0 | 23.1 | 2.6 | 71.8 | 0 | 57.1 | 20.0 | 20.0 | 0 |
| 90th day | 65.2 | 4.4 | 30.4 | 0.0 | 68.8 | 31.2 | 0.0 | 0 | 22.8 | 8.6 | 68.6 | 0 | 60.9 | 30.4 | 4.4 | 0 |
| Average | 44.0 | 6.7 | 47.7 | 1.0 | 34.2 | 12.7 | 52.8 | 0 | 25.0 | 11.2 | 63.0 | 0 | 63.7 | 17.7 | 16.5 | 0 |

| Sample | B 1 | | | | B 3 | | | | B 4 | | | | B 5 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Acid-coagulating | Acid-forming | Inert | Alkali-forming |
| Mix | 51.9 | 25.0 | 19.3 | 1.9 | 45.5 | 22.7 | 27.3 | 4.5 | 51.1 | 9.0 | 6.6 | 31.1 | 71.4 | 23.8 | 0.0 | 0 |
| 8th day | 65.1 | 27.9 | 7.0 | 0.0 | 43.4 | 15.1 | 41.5 | 0.0 | 66.7 | 26.2 | 4.7 | 2.4 | 69.7 | 15.2 | 12.1 | 0 |
| 17th day | 38.2 | 20.6 | 41.2 | 0.0 | 58.6 | 13.8 | 24.1 | 0.0 | 64.0 | 16.0 | 16.0 | 4.0 | 50.0 | 15.4 | 26.9 | 0 |
| 29th day | 50.0 | 27.3 | 20.5 | 2.2 | 29.4 | 38.2 | 32.4 | 0.0 | 52.5 | 32.5 | 15.0 | 0.0 | 61.3 | 25.8 | 12.9 | 0 |
| 45th day | 21.6 | 40.6 | 37.8 | 0.0 | 47.3 | 23.7 | 29.0 | 0.0 | 26.7 | 53.3 | 20.0 | 0.0 | 81.4 | 11.6 | 4.7 | 0 |
| 60th day | 40.4 | 27.7 | 31.9 | 0.0 | 26.7 | 40.0 | 31.1 | 2.2 | 72.0 | 26.0 | 2.0 | 0.0 | 85.7 | 12.5 | 0.0 | 0 |
| 75th day | 40.6 | 27.0 | 32.4 | 0.0 | 53.2 | 14.9 | 31.9 | 0.0 | 53.8 | 35.9 | 10.3 | 0.0 | 53.7 | 43.9 | 2.4 | 0 |
| 90th day | 17.0 | 76.0 | 7.0 | 0.0 | 50.0 | 46.3 | 1.9 | 0.0 | 89.3 | 10.7 | 0.0 | 0.0 | 70.0 | 30.0 | 0.0 | 0 |
| Average | 40.6 | 34.0 | 24.7 | 0.5 | 44.3 | 26.8 | 27.4 | 0.8 | 59.5 | 26.2 | 9.3 | 4.7 | 67.9 | 22.3 | 7.4 | 0 |

| Sample | A 5 | B 5 |
|---|---|---|
| | Peptonizing | Peptonizing |
| Mix | 0.0 | 4.8 |
| 8th day | 4.0 | 3.0 |
| 17th day | 0.0 | 7.7 |
| 29th day | 0.0 | 0.0 |
| 45th day | 0.0 | 2.3 |
| 60th day | 5.4 | 1.8 |
| 75th day | 2.9 | 0.0 |
| 90th day | 4.3 | 0.0 |
| Average | 2.1 | 2.4 |

TABLE 5 (*concluded*)

| Sample | C 3 | | | | | C 4 | | | | | C 5 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing |
| Mix | 61.0 | 4.9 | 31.7 | 0 | 2.4 | 16.7 | 77.8 | 5.5 | 0 | 0.0 | 6.3 | 87.5 | 6.2 | 0.0 | 0.0 |
| 8th day | 38.9 | 38.9 | 22.2 | 0 | 0.0 | 24.0 | 68.0 | 8.0 | 0 | 0.0 | 14.8 | 81.5 | 3.7 | 0.0 | 0.0 |
| 17th day | 41.3 | 41.3 | 17.4 | 0 | 0.0 | 3.2 | 93.6 | 0.0 | 0 | 3.2 | 11.5 | 61.6 | 23.1 | 0.0 | 3.8 |
| 29th day | 40.5 | 50.0 | 7.1 | 0 | 2.4 | 41.4 | 55.2 | 3.4 | 0 | 0.0 | 19.2 | 80.8 | 0.0 | 0.0 | 0.0 |
| 45th day | 48.9 | 39.5 | 11.6 | 0 | 0.0 | .... | .... | .... | .... | .... | 34.0 | 66.0 | 0.0 | 0.0 | 0.0 |
| 60th day | 67.7 | 25.8 | 6.5 | 0 | 0.0 | 3.6 | 89.2 | 3.6 | 0 | 3.6 | 12.9 | 80.7 | 3.2 | 0.0 | 3.2 |
| 75th day | 56.3 | 29.1 | 14.6 | 0 | 0.0 | 21.9 | 78.1 | 0.0 | 0 | 0.0 | 10.7 | 89.3 | 0.0 | 0.0 | 0.0 |
| 90th day | 74.1 | 18.5 | 7.4 | 0 | 0.0 | 56.3 | 37.5 | 0.0 | 0 | 6.2 | 36.4 | 45.4 | 0.0 | 9.1 | 9.1 |
| Average | 53.6 | 31.0 | 14.8 | 0 | 0.6 | 23.9 | 71.3 | 2.9 | 0 | 1.9 | 18.3 | 74.1 | 4.5 | 1.1 | 2.0 |

| Sample | D 3 | | | | | D 4 | | | | | D 5 | | | | | Average of all samples | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing |
| Mix | 34.8 | 52.2 | 4.3 | 0 | 8.7 | 56.0 | 40.0 | 4.0 | 0 | 0.0 | 56.4 | 35.9 | 5.1 | 0 | 2.6 | 41.2 | 32.1 | 21.4 | 3.2 | 2.1 |
| 8th day | 36.7 | 36.7 | 23.3 | 0 | 3.3 | 95.8 | 2.1 | 0.0 | 0 | 2.1 | 55.3 | 31.6 | 13.1 | 0 | 0.0 | 46.9 | 28.2 | 23.7 | 0.2 | 1.0 |
| 17th day | 60.9 | 13.0 | 26.1 | 0 | 0.0 | 87.9 | 3.0 | 9.1 | 0 | 0.0 | 81.2 | 14.6 | 4.2 | 0 | 0.0 | 49.8 | 23.7 | 24.7 | 0.3 | 1.5 |
| 29th day | 27.0 | 24.3 | 43.3 | 0 | 5.4 | 57.8 | 35.5 | 6.7 | 0 | 0.0 | 53.3 | 31.1 | 15.6 | 0 | 0.0 | 42.5 | 31.7 | 25.0 | 0.2 | 0.6 |
| 45th day | 38.3 | 23.5 | 38.2 | 0 | 0.0 | 26.5 | 28.6 | 42.9 | 0 | 2.0 | 50.8 | 34.4 | 13.1 | 0 | 1.7 | 42.7 | 27.6 | 29.2 | 0.0 | 0.5 |
| 60th day | 38.5 | 26.9 | 30.8 | 0 | 3.8 | 94.6 | 5.4 | 0.0 | 0 | 0.0 | 97.8 | 2.2 | 0.0 | 0 | 0.0 | 49.5 | 26.0 | 23.1 | 0.1 | 1.3 |
| 75th day | 41.4 | 27.6 | 20.7 | 0 | 10.3 | 92.4 | 3.8 | 0.0 | 0 | 3.8 | 86.4 | 13.6 | 0.0 | 0 | 0.0 | 47.2 | 28.8 | 22.6 | 0.0 | 1.4 |
| 90th day | 56.5 | 8.7 | 34.8 | 0 | 0.0 | 5.2 | 94.8 | 0.0 | 0 | 0.0 | 0.0 | 80.0 | 15.0 | 0 | 5.0 | 48.0 | 37.3 | 12.1 | 0.7 | 1.9 |
| Average | 41.8 | 26.6 | 27.7 | 0 | 3.9 | 64.5 | 26.7 | 7.8 | 0 | 1.0 | 60.1 | 30.4 | 8.3 | 0 | 1.2 | 46.0 | 29.4 | 22.7 | 0.6 | 1.3 |

and eleven sets shows a total acid group of 75.4 per cent. Of the total number, 46 per cent belong to the acid-coagulating group, 29.4 per cent to the acid-forming group, 22.7 per cent to the inert group, 0.6 per cent to the alkali-forming group, and 1.3 per cent to the peptonizing group.

The averages of the fourteen samples at the different periods show no uniform tendency to increase or to decrease during storage. This fact, considered in connection with the total counts at these different periods as shown in table 1, indicates that there may be a slow growth of the various groups of organisms during the first week or ten days of storage and that after that time the bacteria present merely live in an inactive state, with a gradual dying-off of all groups. The breaking apart of clumps of bacteria is another possible explanation of the increase in count during the first days of storage. Whether or not this is probable was not determined.

The difference in percentages of bacteria in the groups from the ice cream made of raw cream and in those from the ice cream made of pasteurized cream is shown in table 6. The most noticeable difference is that in all except one sample the pasteurized-cream group shows but few inert bacteria as compared to the raw-cream group. There is at the same time an increase in the total acid group, in some cases appearing in the acid-coagulating group and in other cases in the acid-forming group.

TABLE 6. Percentages of Bacteria in Various Groups as Shown by Litmus Milk Tubes, from Ice Cream Made of Raw and of Pasteurized Cream

| Sample | Raw cream | | | | | Pasteurized cream | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing | Acid-coagulating | Acid-forming | Inert | Alkali-forming | Peptonizing |
| A 3 | 34.2 | 12.7 | 52.8 | 0.0 | 0.3 | ..... | ..... | ..... | ..... | ..... |
| A 4 | ..... | ..... | .... | ..... | ..... | 25.0 | 11.2 | 63.0 | 0.0 | 0.8 |
| A 5 | ..... | ..... | .... | ..... | ..... | 63.7 | 17.7 | 16.5 | 0.0 | 2.1 |
| B 3 | 44.3 | 26.8 | 27.4 | 0.8 | 0.7 | ..... | ..... | ..... | ..... | ..... |
| B 4 | ..... | ..... | .... | ..... | ..... | 59.5 | 26.2 | 9.3 | 4.7 | 0.3 |
| B 5 | ..... | ..... | .... | ..... | ..... | 67.9 | 22.3 | 7.4 | 0.0 | 2.4 |
| C 3 | 53.6 | 31.0 | 14.8 | 0.0 | 0.6 | ..... | ..... | ..... | ..... | ..... |
| C 4 | ..... | ..... | .... | ..... | ..... | 23.9 | 71.3 | 2.9 | 0.0 | 1.9 |
| C 5 | ..... | ..... | .... | ..... | ..... | 18.3 | 74.1 | 4.5 | 1.1 | 2.0 |
| D 3 | 41.8 | 26.6 | 27.7 | 0.0 | 3.9 | ..... | ..... | ..... | ..... | ..... |
| D 4 | ..... | ..... | .... | ..... | ..... | 64.5 | 26.7 | 7.8 | 0.0 | 1.0 |
| D 5 | ..... | ..... | .... | ..... | ..... | 60.1 | 30.4 | 8.3 | 0.0 | 1.2 |
| Average | 43.4 | 24.3 | 30.7 | 0.2 | 1.4 | 47.9 | 35.0 | 14.9 | 0.7 | 1.5 |

TABLE 7. NUMBERS OF BACTERIA OF BACILLUS COLI GROUP AS SHOWN BY ENDO'S MEDIUM

(In bacteria per gram)

| Sample | A 1 | A 3 | A 4 | A 5 | B 1 | B 3 | B 4 | B 5 | C 3 | C 4 | C 5 | D 3 | D 4 | D 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mix | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 2,400 | 0 | 0 | 720 | 25 | 0 |
| 8th day | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 2,500 | 5 | 0 | 715 | 20 | 0 |
| 17th day | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 450 | 0 | 0 | 350 | 5 | 0 |
| 29th day | 200 | 200 | 1,000 | 0 | 8,000 | 10,000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 45th day | 250 | 150 | 535 | 0 | 6,250 | 8,000 | 0 | 0 | 0 | 0 | 0 | 215 | 0 | 0 |
| 60th day | 0 | 0 | 115 | 0 | 310 | 280 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 75th day | 0 | 30 | 0 | 0 | 40 | 250 | 0 | 0 | 0 | 0 | 0 | 75 | 0 | 15 |
| 90th day | 260 | 10 | 55 | 0 | 40 | 200 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*The Bacillus coli group*

Since the presence in any considerable number of members of the *Bacillus coli* group in dairy products is looked upon with suspicion, platings were made at various periods on Endo's medium, to determine whether or not organisms of this class would develop in ice cream during storage. The numbers found in the different samples at various intervals are given in table 7. This shows no increase, but on the contrary a decided falling off, in numbers of bacteria during storage.

*Groups as shown by litmus gelatin and by litmus milk compared*

In order to compare in a general way the groups of bacteria as shown by litmus gelatin plates and by litmus milk tubes, the five groups from the milk tubes were reduced to three by combining the two acid-forming groups and including the alkali-forming with the inert group. The liquefiers of gelatin are here compared to the peptonizers of milk. The comparisons are shown in tables 8 to 16, inclusive, table 16 being a summary of the eight tables preceding.

TABLE 8. Comparison of the Mixes

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 0.8 | 35.3 | 85.3 | 62.7 | 13.9 | 2.0 |
| A 3 | 87.5 | 26.2 | 6.3 | 71.4 | 6.2 | 2.4 |
| A 4 | 66.1 | 94.3 | 30.3 | 3.8 | 3.6 | 1.9 |
| A 5 | ..... | 40.0 | ..... | 60.0 | ..... | 0.0 |
| B 1 | 85.3 | 76.9 | 13.2 | 21.2 | 1.5 | 1.9 |
| B 3 | 87.9 | 68.2 | 9.1 | 31.8 | 3.0 | 0.0 |
| B 4 | 64.8 | 60.1 | 31.0 | 37.7 | 4.2 | 2.2 |
| B 5 | 70.0 | 95.2 | 20.0 | 0.0 | 10.0 | 4.8 |
| C 3 | 97.6 | 65.9 | 0.0 | 31.7 | 2.4 | 2.4 |
| C 4 | 67.3 | 94.5 | 30.7 | 5.5 | 2.0 | 0.0 |
| C 5 | 85.8 | 93.8 | 14.2 | 6.2 | 0.0 | 0.0 |
| D 3 | 79.0 | 87.0 | 9.4 | 4.3 | 11.6 | 8.7 |
| D 4 | 75.0 | 96.0 | 12.5 | 4.0 | 12.5 | 0.0 |
| D 5 | 80.0 | 92.3 | 15.0 | 5.1 | 5.0 | 2.6 |
| Average | 72.9 | 73.3 | 21.3 | 24.6 | 5.8 | 2.1 |

TABLE 9. COMPARISON OF THE EIGHTH-DAY SAMPLES

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 80.0 | 57.7 | 16.0 | 42.3 | 4.0 | 0.0 |
| A 3 | 79.5 | 42.9 | 11.7 | 57.1 | 8.8 | 0.0 |
| A 4 | 90.0 | 25.4 | 10.0 | 72.5 | 0.0 | 2.1 |
| A 5 | 77.7 | 72.0 | 22.3 | 24.0 | 0.0 | 4.0 |
| B 1 | 96.2 | 93.0 | 1.3 | 7.0 | 2.5 | 0.0 |
| B 3 | 90.0 | 58.5 | 3.4 | 41.5 | 6.6 | 0.0 |
| B 4 | 55.0 | 92.9 | 45.0 | 7.1 | 0.0 | 0.0 |
| B 5 | 85.7 | 84.9 | 14.3 | 12.1 | 0.0 | 3.0 |
| C 3 | 89.7 | 77.8 | 7.8 | 22.2 | 2.5 | 0.0 |
| C 4 | 85.6 | 92.0 | 14.4 | 8.0 | 0.0 | 0.0 |
| C 5 | 78.2 | 96.3 | 21.8 | 3.7 | 0.0 | 0.0 |
| D 3 | 92.3 | 73.4 | 5.1 | 23.3 | 2.6 | 3.3 |
| D 4 | 82.5 | 97.9 | 17.5 | 0.0 | 0.0 | 2.1 |
| D 5 | 63.6 | 86.9 | 36.4 | 13.1 | 0.0 | 0.0 |
| Average | 81.9 | 75.1 | 16.2 | 23.9 | 1.9 | 1.0 |

TABLE 10. COMPARISON OF THE SEVENTEENTH-DAY SAMPLES

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 50.0 | 58.9 | 25.0 | 38.5 | 25.0 | 2.6 |
| A 3 | 100.0 | 51.0 | 0.0 | 49.0 | 0.0 | 0.0 |
| A 4 | 70.0 | 37.2 | 20.0 | 62.8 | 10.0 | 0.0 |
| A 5 | 93.3 | 92.9 | 2.8 | 7.1 | 3.9 | 0.0 |
| B 1 | 93.6 | 58.8 | 6.4 | 41.2 | 0.0 | 0.0 |
| B 3 | 100.0 | 72.4 | 0.0 | 24.1 | 0.0 | 3.5 |
| B 4 | 80.0 | 80.0 | 20.0 | 20.0 | 0.0 | 0.0 |
| B 5 | 100.0 | 65.4 | 0.0 | 26.9 | 0.0 | 7.7 |
| C 3 | ..... | 82.6 | ..... | 17.4 | ..... | 0.0 |
| C 4 | 80.0 | 96.8 | 0.0 | 0.0 | 20.0 | 3.2 |
| C 5 | 84.2 | 73.1 | 10.6 | 23.1 | 5.2 | 3.8 |
| D 3 | 94.5 | 73.9 | 3.7 | 26.1 | 1.8 | 0.0 |
| D 4 | 93.8 | 90.9 | 6.2 | 9.1 | 0.0 | 0.0 |
| D 5 | 95.6 | 95.8 | 2.2 | 4.2 | 2.2 | 0.0 |
| Average | 87.3 | 73.5 | 7.5 | 25.0 | 5.2 | 1.5 |

TABLE 11. Comparison of the Twenty-ninth-Day Samples

| Samples | Acid | | Inert | | Liquefiers | Pepto-nizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 76.4 | 56.4 | 11.9 | 43.6 | 11.7 | 0.0 |
| A 3 | 89.4 | 26.5 | 8.0 | 73.5 | 2.6 | 0.0 |
| A 4 | 81.8 | 26.1 | 18.2 | 73.9 | 0.0 | 0.0 |
| A 5 | 94.6 | 97.2 | 2.4 | 2.8 | 3.0 | 0.0 |
| B 1 | 98.0 | 77.3 | 1.0 | 22.7 | 1.0 | 0.0 |
| B 3 | 91.7 | 67.6 | 0.0 | 32.4 | 8.3 | 0.0 |
| B 4 | 92.1 | 85.0 | 6.8 | 15.0 | 1.1 | 0.0 |
| B 5 | 93.1 | 87.1 | 6.9 | 12.9 | 0.0 | 0.0 |
| C 3 | 95.5 | 90.5 | 3.4 | 7.1 | 1.1 | 2.4 |
| C 4 | 80.0 | 96.6 | 20.0 | 3.4 | 0.0 | 0.0 |
| C 5 | 85.0 | 100.0 | 15.0 | 0.0 | 0.0 | 0.0 |
| D 3 | 97.1 | 51.3 | 1.0 | 43.3 | 1.9 | 5.4 |
| D 4 | 95.1 | 93.3 | 4.9 | 6.7 | 0.0 | 0.0 |
| D 5 | 93.9 | 84.4 | 6.1 | 15.6 | 0.0 | 0.0 |
| Average | 90.3 | 74.2 | 7.5 | 25.2 | 2.2 | 0.6 |

TABLE 12. Comparison of the Forty-fifth-Day Samples

| Samples | Acid | | Inert | | Liquefiers | Pepto-nizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 87.5 | 44.0 | 0.0 | 56.0 | 12.5 | 0.0 |
| A 3 | 76.9 | 47.1 | 23.1 | 52.9 | 0.0 | 0.0 |
| A 4 | 82.4 | 35.5 | 17.6 | 64.5 | 0.0 | 0.0 |
| A 5 | 62.5 | 91.3 | 12.5 | 8.7 | 25.0 | 0.0 |
| B 1 | 92.9 | 62.2 | 7.1 | 37.8 | 0.0 | 0.0 |
| B 3 | 82.7 | 71.0 | 13.9 | 29.0 | 3.4 | 0.0 |
| B 4 | 75.0 | 8.00 | 18.8 | 20.0 | 6.2 | 0.0 |
| B 5 | 76.9 | 93.0 | 8.0 | 4.7 | 15.1 | 2.3 |
| C 3 | ..... | 88.4 | ..... | 11.6 | ..... | 0.0 |
| C 4 | 90.4 | ..... | 9.6 | ..... | 0.0 | ..... |
| C 5 | 8.00 | 100.0 | 20.0 | 0.0 | 0.0 | 0.0 |
| D 3 | 94.8 | 61.8 | 3.9 | 38.2 | 1.3 | 0.0 |
| D 4 | 97.4 | 55.1 | 1.7 | 42.9 | 0.9 | 2.0 |
| D 5 | 4.9 | 85.2 | 91.5 | 13.1 | 3.6 | 1.7 |
| Average | 77.3 | 70.3 | 17.5 | 29.2 | 5.2 | 0.5 |

TABLE 13. COMPARISON OF THE SIXTIETH-DAY SAMPLES

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 91.6 | 35.0 | 4.3 | 65.0 | 4.1 | 0.0 |
| A 3 | 95.5 | 42.2 | 0.0 | 57.8 | 4.5 | 0.0 |
| A 4 | 60.0 | 13.7 | 13.3 | 86.3 | 26.7 | 0.0 |
| A 5 | 80.3 | 89.2 | 16.7 | 5.4 | 3.0 | 5.4 |
| B 1 | 82.1 | 68.1 | 17.9 | 31.9 | 0.0 | 0.0 |
| B 3 | 98.3 | 66.7 | 1.7 | 33.3 | 0.0 | 0.0 |
| B 4 | 95.4 | 98.0 | 4.6 | 2.0 | 0.0 | 0.0 |
| B 5 | 83.3 | 98.2 | 16.7 | 0.0 | 0.0 | 1.8 |
| C 3 | 90.0 | 93.5 | 9.2 | 6.5 | 0.8 | 0.0 |
| C 4 | 66.7 | 92.8 | 33.3 | 3.6 | 0.0 | 3.6 |
| C 5 | 60.0 | 93.6 | 40.0 | 3.2 | 0.0 | 3.2 |
| D 3 | 92.0 | 65.4 | 8.0 | 30.8 | 0.0 | 3.8 |
| D 4 | 65.6 | 100.0 | 34.4 | 0.0 | 0.0 | 0.0 |
| D 5 | 81.4 | 100.0 | 18.6 | 0.0 | 0.0 | 0.0 |
| Average | 81.6 | 75.5 | 15.6 | 23.2 | 2.8 | 1.3 |

TABLE 14. COMPARISON OF THE SEVENTY-FIFTH-DAY SAMPLES

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 87.5 | 48.7 | 12.5 | 51.3 | 0.0 | 0.0 |
| A 3 | 80.0 | 39.5 | 15.0 | 60.5 | 5.0 | 0.0 |
| A 4 | 88.8 | 25.7 | 11.2 | 71.8 | 0.0 | 2.5 |
| A 5 | 60.7 | 77.1 | 37.7 | 20.0 | 1.6 | 2.9 |
| B 1 | 96.2 | 67.6 | 2.6 | 32.4 | 1.2 | 0.0 |
| B 3 | 92.0 | 68.1 | 6.0 | 31.9 | 2.0 | 0.0 |
| B 4 | 88.8 | 89.7 | 11.2 | 10.3 | 0.0 | 0.0 |
| B 5 | 77.0 | 97.6 | 19.2 | 2.4 | 3.8 | 0.0 |
| C 3 | 73.0 | 85.4 | 21.6 | 14.6 | 5.4 | 0.0 |
| C 4 | 66.7 | 100.0 | 0.0 | 0.0 | 33.3 | 0.0 |
| C 5 | 40.0 | 100.0 | 30.0 | 0.0 | 30.0 | 0.0 |
| D 3 | 72.2 | 69.0 | 22.3 | 20.7 | 5.5 | 10.3 |
| D 4 | ..... | 96.2 | ..... | 0.0 | ..... | 3.8 |
| D 5 | 45.6 | 100.0 | 26.4 | 0.0 | 28.0 | 0.0 |
| Average | 74.5 | 76.0 | 16.6 | 22.6 | 8.9 | 1.4 |

TABLE 15. Comparison of the Ninetieth-Day Samples

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| A 1 | 81.2 | 69.6 | 12.6 | 30.4 | 6.2 | 0.0 |
| A 3 | 82.6 | 100.0 | 17.4 | 0.0 | 0.0 | 0.0 |
| A 4 | 90.9 | 31.4 | 0.0 | 68.6 | 9.1 | 0.0 |
| A 5 | 67.5 | 91.3 | 25.7 | 4.4 | 6.8 | 4.3 |
| B 1 | 84.1 | 93.0 | 14.3 | 7.0 | 1.6 | 0.0 |
| B 3 | 79.2 | 96.3 | 12.5 | 1.9 | 8.3 | 1.8 |
| B 4 | 78.1 | 100.0 | 12.8 | 0.0 | 9.1 | 0.0 |
| B 5 | 69.2 | 100.0 | 19.3 | 0.0 | 11.5 | 0.0 |
| C 3 | 71.0 | 92.6 | 18.8 | 7.4 | 10.2 | 0.0 |
| C 4 | 59.1 | 93.8 | 27.3 | 0.0 | 13.6 | 6.2 |
| C 5 | ..... | 81.8 | ..... | 9.1 | ..... | 9.1 |
| D 3 | 53.9 | 65.2 | 30.7 | 34.8 | 15.4 | 0.0 |
| D 4 | ..... | 100.0 | ..... | 0.0 | ..... | 0.0 |
| D 5 | ..... | 80.0 | ..... | 15.0 | ..... | 5.0 |
| Average | 74.3 | 85.3 | 17.4 | 12.8 | 8.3 | 1.9 |

TABLE 16. Comparison of the Averages of Samples at Different Periods

| Samples | Acid | | Inert | | Liquefiers | Peptonizers |
|---|---|---|---|---|---|---|
| | Gelatin | Milk | Gelatin | Milk | Gelatin | Milk |
| Mix | 72.9 | 73.3 | 21.3 | 24.6 | 5.8 | 2.1 |
| 8th day | 81.9 | 75.1 | 16.2 | 23.9 | 1.9 | 1.0 |
| 17th day | 87.3 | 73.5 | 7.5 | 25.0 | 5.2 | 1.5 |
| 29th day | 90.3 | 74.2 | 7.5 | 25.2 | 2.2 | 0.6 |
| 45th day | 77.3 | 70.3 | 17.5 | 29.2 | 5.2 | 0.5 |
| 60th day | 81.6 | 75.5 | 15.6 | 23.2 | 2.8 | 1.3 |
| 75th day | 74.5 | 76.0 | 16.6 | 22.6 | 8.9 | 1.4 |
| 90th day | 74.3 | 85.3 | 17.4 | 12.8 | 8.3 | 1.9 |

The gelatin plates show the higher proportion of acid formers in all periods except the mix, the seventy-fifth day, and the ninetieth day, and a higher proportion of liquefiers than of peptonizers from milk tubes at every period. Undoubtedly there were some colonies which liquefied gelatin but did not peptonize milk. With these two groups larger in the

gelatin than the corresponding ones of the milk tubes, the inert group, of course, must be smaller. In only one case, on the ninetieth day, did the gelatin show as high a percentage in the inert group as did the milk tubes.

### ORGANISMS SURVIVING ONE HUNDRED AND TWENTY DAYS OF STORAGE

For a more detailed study of the classes and types of bacteria which survived storage, twenty typical colonies were picked from a representative agar plate of each of the fourteen samples plated on the one hundred and twentieth day.. These colonies were first transferred to fermentation tubes of lactose bouillon. From these tubes stained slides were made and examined under the microscope, and transfers were made to gelatin stabs, agar slants, and litmus milk tubes. All were incubated at 20° C., the agar plates for seven days, the lactose bouillon and agar slants for five days, and the gelatin stabs and litmus milk tubes for fifteen days. A record was kept of all daily changes during these periods.

TABLE 17. GROUPS AND TYPES OF ORGANISMS SURVIVING 120 DAYS OF STORAGE

| Groups or types of organisms | Number from six raw samples | Number from eight pasteurized samples | Total number |
|---|---|---|---|
| *Bacterium lactis acidi* group | | | |
| Coagulated milk in 1 to 4 days | 31 | 2 | 33 |
| Coagulated milk in 5 to 10 days | 7 | 3 | 10 |
| Coagulated milk in 11 to 15 days | 7 | 8 | 15 |
| Milk not coagulated in 15 days | 69 | 126 | 195 |
| Appearing in long chains, acid formers but with no coagulation | 2 | 8 | 10 |
| Total | 116 | 147 | 263 |
| Bacteria, forming acid and liquefying gelatin | 0 | 4 | 4 |
| Cocci, forming acid, yellow growth on agar | 0 | 2 | 2 |
| Cocci, no action in milk | 1 | 1 | 2 |
| Diplococci, peptonizing milk and liquefying gelatin | 1 | 0 | 1 |
| Long rods, peptonizing milk and liquefying gelatin | 1 | 3 | 4 |
| Long rods, alkali producers | 1 | 1 | 2 |
| Streptothrix | 0 | 1 | 1 |
| Mold | 0 | 1 | 1 |
| Total miscellaneous | 4 | 13 | 17 |

Of the 280 cultures 269 were acid producers, 263 of these apparently belonging to the *Bacterium lactis acidi* group. These varied from small rods which could scarcely be distinguished from cocci, to slightly larger distinct rods. Many formed short chains, but only ten appeared in long chains.

For comparison, a sample of good commercial starter was plated and colonies were examined and grown as described. Little difference could be noted between these acid-forming organisms and those isolated from the storage ice cream. In many cases they appeared to be identical.

The numbers of the various groups and types of organisms appearing among these 280 cultures are given in table 17.

### Influence of incubation temperatures on the total counts

Before starting to make bacteria counts of experimental freezings of ice cream, it was deemed best to determine the incubation temperature most favorable to the growth of such bacteria in plates. For this purpose lactose agar of the composition previously mentioned was chosen as the nutrient medium. Twenty-two samples of ice cream were procured from nine manufacturers, and were plated in three dilutions. Four sets of plates in duplicate were made from each dilution, and each set was incubated at a different temperature. The temperature and the time of incubation were as follows:

Two days at 37° C. on all samples;
Five days at 30° C. on all samples;
Seven days at 20° C. on all samples;
Thirty days at 0° C. and two days at 37° C. on samples C to P inclusive;
Five days at 20° C. and two days at 37° C. on samples Q to W inclusive.

The results are shown in table 18. It will be noted that the average count of these samples from plates incubated at 30° C. for five days was almost two and one-half times the count of the same samples from plates incubated at 37° C. for two days. In no case did the 37° plates show as high a count as the 30° plates. The plates incubated at 20° C. showed an average count three times as great as those incubated at 37° C. In this case the 20° plates gave a higher count than the 30° plates in seventeen cases, while the 30° plates gave higher results in only five cases.

TABLE 18. EFFECT OF DIFFERENT TEMPERATURES OF INCUBATION OF PLATES ON THE TOTAL COUNT OF BACTERIA IN ICE CREAM

| Sample | Time and temperature of incubation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Two days at 37° C. | Per cent | Five days at 30° C. | Per cent | Seven days at 20° C. | Per cent | Thirty days at 0° C. and two days at 37° C. | Per cent | Five days at 20° C. and two days at 37° C. | Per cent |
| A | 285,000 | 100 | 520,000 | 182.4 | 675,000 | 236.8 | ..... | ..... | ..... | ..... |
| B | 7,750,000 | 100 | 14,550,000 | 187.7 | 16,500,000 | 212.9 | ..... | ..... | ..... | ..... |
| C | 590,000 | 100 | 1,580,000 | 267.8 | 1,695,000 | 287.3 | 315,000 | 53.4 | ..... | ..... |
| D | 2,850,000 | 100 | 6,900,000 | 242.1 | 5,460,000 | 191.6 | 830,000 | 29.1 | ..... | ..... |
| E | 1,985,000 | 100 | 4,222,500 | 212.7 | 4,125,000 | 207.8 | 340,000 | 17.1 | ..... | ..... |
| F | 360,000 | 100 | 495,000 | 137.5 | 520,000 | 144.4 | 75,000 | 20.8 | ..... | ..... |
| G | 1,815,000 | 100 | 8,950,000 | 493.1 | 10,550,000 | 581.3 | 6,860,000 | 378.0 | ..... | ..... |
| H | 4,910,000 | 100 | 12,500,000 | 254.6 | 14,950,000 | 304.5 | 4,215,000 | 85.8 | ..... | ..... |
| I | 3,095,000 | 100 | 10,650,000 | 344.1 | 10,550,000 | 340.9 | 5,315,000 | 171.7 | ..... | ..... |
| J | 2,453,000 | 100 | 4,420,000 | 180.2 | 4,655,000 | 189.8 | 820,000 | 33.4 | ..... | ..... |
| L | 39,900,000 | 100 | 48,500,000 | 121.5 | 56,800,000 | 142.3 | 50,133,133 | 125.6 | ..... | ..... |
| M | 300,000 | 100 | 1,600,000 | 533.3 | 2,802,500 | 934.2 | 260,000 | 86.7 | ..... | ..... |
| N | 11,900,000 | 100 | 35,400,000 | 297.5 | 70,500,000 | 592.4 | 7,250,000 | 60.9 | ..... | ..... |
| O | 77,000,000 | 100 | 125,000,000 | 162.3 | 183,500,000 | 238.3 | 182,000,000 | 236.4 | ..... | ..... |
| P | 4,630,000 | 100 | 6,750,000 | 145.8 | 5,950,000 | 128.5 | 5,195,000 | 112.2 | ..... | ..... |
| Q | 10,300,000 | 100 | 27,250,000 | 264.6 | 26,233,333 | 254.7 | ..... | ..... | 27,100,000 | 263.1 |
| R | 2,245,000 | 100 | 3,703,333 | 164.9 | 5,750,000 | 256.1 | ..... | ..... | 5,750,000 | 256.1 |
| S | 580,000 | 100 | 995,000 | 171.5 | 1,340,000 | 231.0 | ..... | ..... | 1,410,000 | 243.1 |
| T | 8,273,333 | 100 | 38,750,000 | 468.4 | 47,775,000 | 577.4 | ..... | ..... | 39,466,666 | 477.0 |
| U | 12,250,000 | 100 | 22,833,333 | 186.4 | 34,850,000 | 284.5 | ..... | ..... | 33,700,000 | 275.1 |
| V | 1,780,000 | 100 | 3,782,500 | 212.5 | 4,953,333 | 278.3 | ..... | ..... | 4,393,333 | 246.8 |
| W | 106,500,000 | 100 | 160,500,000 | 150.7 | 198,500,000 | 186.4 | ..... | ..... | 157,000,000 | 147.4 |
| Average of 22 samples | ..... | 100 | ..... | 244.6 | ..... | 309.2 | ..... | ..... | ..... | ..... |
| Average of 13 samples | ..... | 100 | ..... | 261.0 | ..... | 329.5 | ..... | 108.5 | ..... | ..... |
| Average of 7 samples | ..... | 100 | ..... | 231.3 | ..... | 295.5 | ..... | ..... | ..... | 272.7 |

The 0°-37° plates from thirteen samples gave a lower count than the 20° plates in every case, and a lower count than the 37° plates in eight of the thirteen trials.

Comparison of the 20°-37° plates with the 20° plates seemed to show that there was no advantage in incubating at higher temperatures after removing the plates from the 20° incubator.

Because of these results it was decided to incubate the plates from the experimental samples of ice cream at 20° C. for seven days, this temperature tending to show more nearly the true number of bacteria present than any of the other temperatures used.

### Numbers of bacteria found in ice-cream gelatin prepared by different methods

Three of the commonest methods of dissolving gelatin for use in ice cream are as follows: (1) soaking in cold water for about thirty minutes, then heating to from 125° to 130° F. until dissolved; (2) soaking in cold water for thirty minutes, then heating to from 160° to 170° F.; (3) pouring the gelatin into boiling water and stirring it until dissolved.

In order to determine the effect of these methods on the bacteria content, fifteen samples of gelatin were procured from various manufacturers and dealers and were prepared by each of the methods. Platings from each preparation were made on litmus lactose gelatin and incubated at 20° C. The results are shown in table 19. The average total count of the fifteen samples when dissolved at a temperature of from 125° to 130° F. was 388,162; when dissolved at from 160° to 170° F. the average was only 1172; and when dissolved in boiling water the count was further reduced to an average of 530. On the other hand, the proportion of liquefiers relative to the total count was in most cases increased with the higher temperature. Occasionally the jelly from gelatin dissolved in boiling water had a slightly disagreeable flavor, and if it was held at this temperature for a considerable time some of the jellying power seemed to be destroyed. It therefore seemed best to prepare the gelatin for the experimental batches of ice cream by the second method — soaking in cold water, and then heating to from 160° to 170° F. just before using.

TABLE 19. EFFECT OF DIFFERENT METHODS OF DISSOLVING GELATIN ON THE BACTERIA COUNT

(The numbers expressed are in terms of bacteria in one gram of dry gelatin)

| Sample | Method 1 — dissolving at 125° to 130° F. | | | Method 2 — dissolving at 160° to 170° F. | | | Method 3 — dissolving in boiling water | | |
|---|---|---|---|---|---|---|---|---|---|
| | Total count | Number of liquefiers | Per cent of liquefiers | Total count | Number of liquefiers | Per cent of liquefiers | Total count | Number of liquefiers | Per cent of liquefiers |
| A | 430 | 310 | 72.1 | 70 | 5 | 7.1 | 24 | 4 | 16.7 |
| B | 2,396,000 | 6,000 | 0.3 | 380 | 265 | 69.7 | 82 | 64 | 78.0 |
| C | 118,500 | 3,500 | 2.9 | 760 | 385 | 50.7 | 26 | 10 | 38.5 |
| D | 845,000 | 13,500 | 1.6 | 5,700 | 5,700 | 100.0 | 3,200 | 3,200 | 100.0 |
| E | 55,500 | 7,000 | 12.6 | 5,720 | 5,720 | 100.0 | 3,060 | 3,060 | 100.0 |
| G | 91,000 | 0 | 0.0 | 215 | 130 | 60.5 | 105 | 60 | 57.1 |
| H | 19,000 | 1,000 | 5.3 | 200 | 100 | 50.0 | 5 | 0 | 0.0 |
| I | 21,000 | 1,000 | 4.8 | 485 | 190 | 39.2 | 60 | 0 | 0.0 |
| J | 54,000 | 7,000 | 13.0 | 1,030 | 1,030 | 100.0 | 540 | 540 | 100.0 |
| K | 159,000 | 9,000 | 5.7 | 1,440 | 1,440 | 100.0 | 470 | 470 | 100.0 |
| L | 2,016,000 | 6,500 | 0.3 | 300 | 270 | 90.0 | 74 | 52 | 70.3 |
| M | 4,500 | 2,000 | 44.4 | 995 | 95 | 9.5 | 234 | 38 | 16.2 |
| N | 15,000 | 500 | 3.3 | 60 | 10 | 16.7 | 14 | 0 | 0.0 |
| O | 25,500 | 2,500 | 9.8 | 185 | 90 | 48.6 | 46 | 2 | 4.3 |
| P | 2,000 | 0 | 0.0 | 35 | 10 | 28.6 | 10 | 2 | 20.0 |
| Average | 388,162 | 3,987 | ..... | 1,172 | 1,029 | ..... | 530 | 500 | ..... |

## A CHECK ON THE ACCURACY OF THE TOTAL COUNTS AS SHOWN IN TABLE 1

A study of table 1 (page 336) shows that the bacteria content of ice cream does not change appreciably during a storage period of reasonable length. In fact, the average counts show as low variation as might reasonably be expected from a number of separate platings from the same sample of almost any dairy product. The question might then arise, do these averages show a normal increase and decrease of the bacteria present in the ice cream, or are they merely coincidences? As a check on this, and also on the method used, the following series of platings were made:

1. Thirteen samples were taken from each of the fourteen cans of ice cream in storage and were plated separately.

2. From one of the thirteen samples from each of the fourteen sets, thirteen weighings and dilutions were made, each being plated separately.

3. From one of the final dilution bottles from each of the fourteen sets, thirteen sets of plates were made.

The results compared to the thirteen averages as shown in table 1, beginning with the frozen ice cream and ending with the sixty-days period

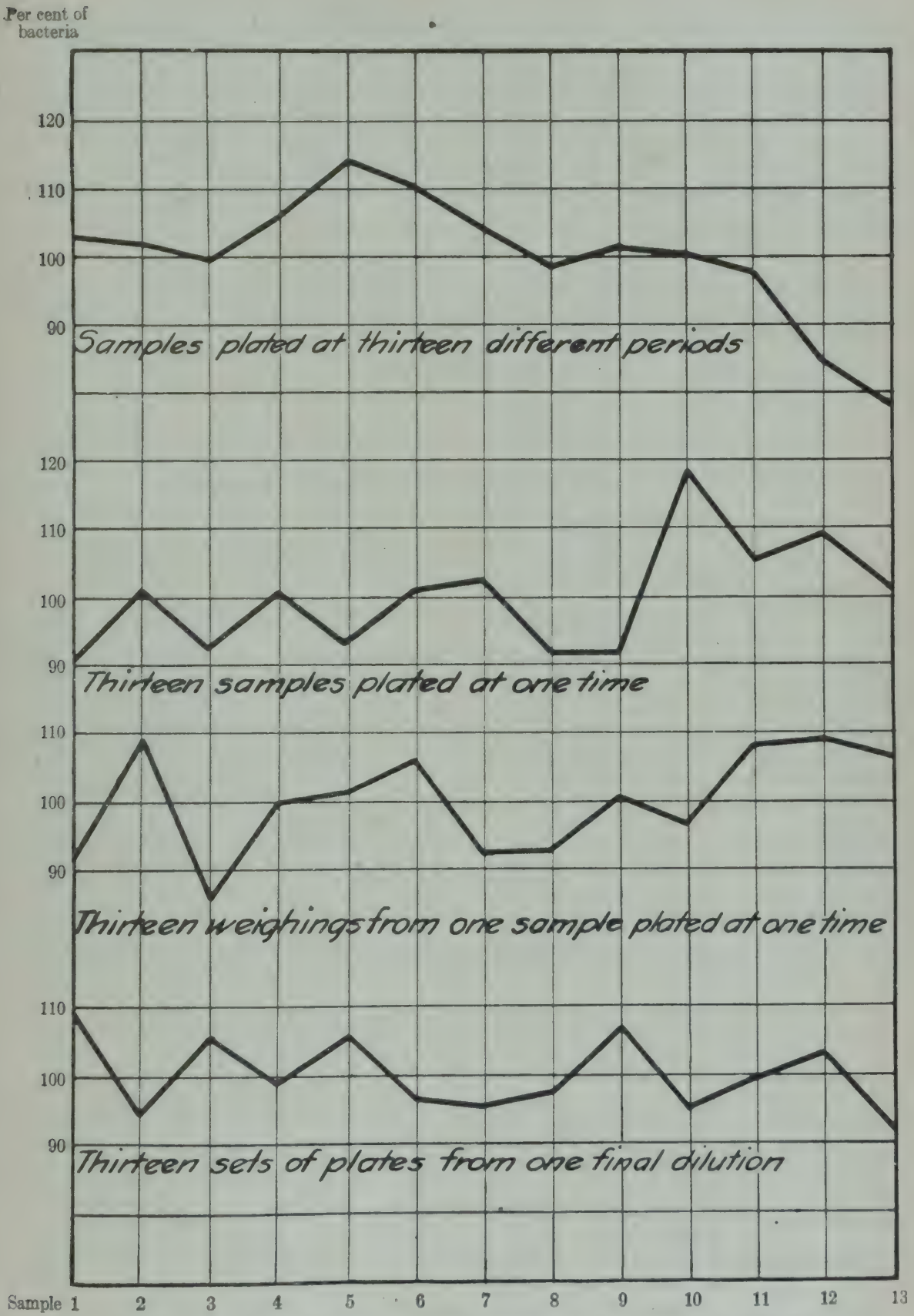


Fig. 76. Comparative results from different platings of ice cream

of storage, are shown in table 20. The same results are shown graphically in figure 76. The curve of the samples plated at different times shows a certain uniformity of increase and decrease; those from the other platings show no uniformity at all, as would naturally be expected. This indicates that the averages in table 1 undoubtedly approximate the real increase and decrease of bacteria in these fourteen samples of ice cream during storage.

TABLE 20. RESULTS OF MAKING THIRTEEN SEPARATE PLATINGS FROM ONE DILUTION, FROM ONE SAMPLE, AND FROM THIRTEEN SAMPLES, COMPARED TO THE SAME NUMBER OF PLATINGS FROM DIFFERENT SAMPLES AT INTERVALS THRUOUT A SIXTY-DAYS PERIOD*

(In bacteria per gram)

| Sample | Average of 14 sets plated at different times during storage (From table 1) | Sample | Average of 14 sets of 13 samples plated at once | Average of 14 sets of 13 weighings from same sample | Average of 14 sets of 13 platings from same dilution |
|---|---|---|---|---|---|
| Fresh | 9,736,750 | 1 | 7,182,833 | 7,937,801 | 8,003,761 |
| 2d day | 9,591,428 | 2 | 8,093,102 | 9,450,696 | 6,919,060 |
| 4th day | 9,342,871 | 3 | 7,325,951 | 7,435,724 | 7,717,189 |
| 6th day | 9,939,982 | 4 | 7,966,278 | 8,654,462 | 7,251,138 |
| 8th day | 10,721,707 | 5 | 7,372,990 | 8,778,560 | 7,718,509 |
| 11th day | 10,363,707 | 6 | 7,992,696 | 9,161,576 | 7,070,531 |
| 14th day | 9,795,532 | 7 | 8,099,049 | 8,018,915 | 6,967,876 |
| 17th day | 9,255,325 | 8 | 7,273,532 | 8,027,714 | 7,164,000 |
| 21st day | 9,546,421 | 9 | 7,250,422 | 8,718,209 | 7,824,028 |
| 25th day | 9,462,750 | 10 | 9,354,286 | 8,371,656 | 6,959,388 |
| 29th day | 9,190,482 | 11 | 8,352,386 | 9,363,786 | 7,287,355 |
| 45th day | 7,941,564 | 12 | 8,649,410 | 9,451,341 | 7,553,016 |
| 60th day | 7,355,549 | 13 | 8,043,486 | 9,252,876 | 6,754,543 |

*The three last columns show lower counts than the first column in most cases, because the platings were made during the 45- to 60-days periods of storage, after the numbers had decreased somewhat.

## PROBABLE ERROR OF THE BACTERIA COUNTS

To further ascertain the accuracy of the technique, a more detailed study of the results of these various sets of platings is required. In table 21 the percentage variation of each individual count from its mean is shown, together with the average deviation, the coefficient of variability, and the probable error in each case, all of which are expressed in percentage. It will be noted that two columns are given to the thirteen

TABLE 21. VARIABILITY OF INDIVIDUAL COUNTS FROM THE MEAN

| Per cent of variation from mean | 14 sets of 13 samples plated at once | | | | | | Number of variates | 14 sets of 13 weighings from same sample | | | | | | Number of variates | 14 sets of 13 platings from same dilution | | | | | | Number of variates | 13 sets of 13 platings from same dilution | | | | | | Number of variates |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | 5 | 5 | 5 | 5 | 2 | 27 | 5 | 5 | 5 | 5 | 4 | ... | 24 | 5 | 5 | 5 | 5 | 5 | 2 | 27 | 5 | 5 | 5 | 5 | 5 | 2 | 27 |
| 3 | 5 | 5 | 5 | 5 | ... | ... | 20 | 5 | 5 | 5 | 5 | 2 | ... | 22 | 5 | 5 | 5 | 5 | ... | ... | 20 | 5 | 5 | 5 | 5 | ... | ... | 20 |
| 5 | 5 | 5 | 5 | 5 | 5 | 2 | 27 | 5 | 5 | 5 | 5 | 5 | ... | 26 | 5 | 5 | 5 | 5 | 5 | 4 | 29 | 5 | 5 | 5 | 5 | 5 | 3 | 28 |
| 7 | 5 | 5 | 5 | 2 | ... | ... | 17 | 5 | 5 | 5 | 2 | ... | 1 | 17 | 5 | 5 | 5 | 3 | ... | ... | 18 | 5 | 5 | 5 | 3 | ... | ... | 18 |
| 9 | 5 | 5 | 3 | ... | ... | ... | 13 | 5 | 5 | 5 | ... | ... | ... | 15 | 5 | 5 | 5 | 1 | ... | ... | 16 | 5 | 5 | 5 | 1 | ... | ... | 16 |
| 11 | 5 | 3 | ... | ... | ... | ... | 8 | 5 | 5 | 1 | ... | ... | ... | 11 | 5 | 5 | 3 | ... | ... | ... | 13 | 5 | 5 | 3 | ... | ... | ... | 13 |
| 13 | 5 | 5 | ... | ... | ... | ... | 10 | 5 | 5 | 3 | ... | ... | ... | 13 | 5 | 5 | ... | ... | ... | ... | 10 | 5 | 5 | ... | ... | ... | ... | 10 |
| 15 | 5 | 5 | 3 | ... | ... | ... | 13 | 5 | 5 | 4 | ... | ... | ... | 14 | 5 | 3 | ... | ... | ... | ... | 8 | 5 | 2 | ... | ... | ... | ... | 7 |
| 17 | 5 | 5 | 1 | ... | ... | ... | 11 | 5 | 1 | ... | ... | ... | ... | 6 | 5 | 5 | 1 | ... | ... | ... | 11 | 5 | 5 | 1 | ... | ... | ... | 11 |
| 19 | 5 | 3 | ... | ... | ... | ... | 8 | 5 | 1 | ... | ... | ... | ... | 6 | 5 | ... | ... | ... | ... | ... | 5 | 5 | ... | ... | ... | ... | ... | 5 |
| 21 | 1 | ... | ... | ... | ... | ... | 1 | 5 | ... | ... | ... | ... | ... | 5 | 4 | ... | ... | ... | ... | ... | 4 | 3 | ... | ... | ... | ... | ... | 3 |
| 23 | 5 | 4 | ... | ... | ... | ... | 9 | 5 | 2 | ... | ... | ... | ... | 7 | 3 | ... | ... | ... | ... | ... | 3 | 2 | ... | ... | ... | ... | ... | 2 |
| 25 | 2 | ... | ... | ... | ... | ... | 2 | 3 | ... | ... | ... | ... | ... | 3 | 1 | ... | ... | ... | ... | ... | 1 | 1 | ... | ... | ... | ... | ... | 1 |
| 27 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | 2 | ... | ... | ... | ... | ... | 2 | 1 | ... | ... | ... | ... | ... | 1 |
| 29 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | 1 | ... | ... | ... | ... | ... | 1 |
| 31 | 3 | ... | ... | ... | ... | ... | 3 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 33 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... |
| 35 | 2 | ... | ... | ... | ... | ... | 2 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... |
| 37 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | 2 | ... | ... | ... | ... | ... | 2 | 1 | ... | ... | ... | ... | ... | 1 |
| 39 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | 2 | ... | ... | ... | ... | ... | 2 | ... | ... | ... | ... | ... | ... | ..... |
| 41 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 43 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 45 | 1 | ... | ... | ... | ... | ... | 1 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 47 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 49 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 51 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 53 | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... |
| 55 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... |
| 57 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... |
| 65 | ... | ... | ... | ... | ... | ... | ..... | ... | ... | ... | ... | ... | ... | ..... | 1 | ... | ... | ... | ... | ... | 1 | ... | ... | ... | ... | ... | ... | ..... |
| Average deviation | 11.04 per cent | | | | | | | 9.74 per cent | | | | | | | 10.36 per cent | | | | | | | 8.44 per cent | | | | | | |
| Coefficient of variability | 15.13 per cent | | | | | | | 12.55 per cent | | | | | | | 14.60 per cent | | | | | | | 10.72 per cent | | | | | | |
| Probable error of single variate | ±10.21 per cent | | | | | | | ± 8.46 per cent | | | | | | | ± 9.85 per cent | | | | | | | ± 7.23 per cent | | | | | | |

platings from the same dilution bottle, one of fourteen sets and the other of thirteen sets. They are the same except that the latter has one set of platings excluded because of their extreme variation, which did not seem to be at all normal when compared to the other sets. While there was no apparent reason for the extreme variation found in this one set of platings, yet, because of the great difference from any other set, it was felt that the average would be more nearly correct if it were excluded. This is borne out by the fact that when this set is not excluded, the sets showed a greater variability than did those of the thirteen separate weighings, which, because of the additional operations involved, would be expected to show the greater variation.

The comparatively narrow limit of the probable error should be noted. As an illustration, if a can of ice cream having a count of 1,000,000 bacteria per gram is considered, the chances are equal that any one sample from that can would give a count somewhere between 1,102,100 and 897,900. This is comparatively close as bacteria counts go. Or, if several weighed portions for dilution were taken from one sample, it is probable that the count would be within the limits of 1,084,600 and 915,400. And again, if several sets of two plates each were poured from the same final dilution, the probable count of any one set would be between 1,072,300 and 927,700.

In pouring plates from the same final dilution, there was only one mechanical operation to cause variation; while in weighing from the same sample separate portions for dilution and plating, there were from eight to eleven distinct operations to cause variation. This was further increased by one when separate samples were taken from the original package for each plating. Therefore, if the variation in counts was caused solely by the technique used, the probable error should be much smaller than is here shown in the case of platings from the same final dilution, or much larger than is shown in the case of platings from separate weighed portions. There seems, then, to be no other way of explaining the variation in the bacterial counts than to charge the greater part of it to the uncertainty of obtaining a uniform distribution of the bacteria in the final dilution water. Of course every dilution would show more or less error in this respect, but the error would greatly increase with the decrease in the number of bacteria present in a given quantity of water,

and therefore it is the final dilution which is the most likely to cause the greatest variation in the count.

In all these comparative platings only two plates were poured in a set, and the counts were calculated from the average of these two. Had more plates been poured and used to determine the counts, it is reasonable to expect that the results would have been more uniform, with a correspondingly lower probable error. To gain an idea of what difference might be expected, the plates in the last series of platings from the final dilution were grouped in sets of four, and the counts, with the probable error of any one count, were calculated on this basis. As before noted, the probable error when sets of two plates each were used was ±7.23 per cent; the probable error when the plates were grouped in sets of four was reduced to ±5.48 per cent.

### Effect of different media on the bacteria count

#### *Lactose agar and litmus lactose gelatin compared*

Thruout these experiments there were one hundred and seventy-seven samples of ice cream plated both on lactose agar and on litmus lactose gelatin. The agar gave the higher count in one hundred and sixty-eight cases, the gelatin in only seven; in two cases the counts were equal. During these platings three different brands of gelatin were used, with practically equal results. The average total count on the agar was 9,193,500 bacteria per gram, while that on the gelatin was 2,773,000, or only 30 per cent of the agar count. This difference was so striking and so uniform that it was thought best to make a series of check platings with plain lactose gelatin, in order to determine whether the difference might be attributed to the use of litmus in the plates.

#### *Litmus lactose gelatin and lactose gelatin compared*

The sixty-five samples comparing litmus lactose gelatin and lactose gelatin showed the higher count to result from the plain lactose gelatin in forty-nine cases and from the litmus lactose gelatin in only fourteen; in two cases the counts were equal. The average plate count on the litmus lactose gelatin was 36, while that on the plain lactose gelatin was 47, an increase of 30 per cent. This indicates that the litmus either has an inhibiting action on the growth of the organisms, or that it makes

the counting more difficult so that some of the small colonies are not seen and therefore not counted.

The litmus solution used in this work was made as follows: Forty grams of litmus cubes were tied in cheesecloth and allowed to soak for twenty-four hours in 300 cubic centimeters of water. The solution was then filtered into small flasks and sterilized. Two cubic centimeters of this solution was added to each plate when poured.

*Lactose agar and lactose gelatin compared*

The next series of comparisons was between lactose agar and lactose gelatin, to determine whether or not the gelatin plates would give lower counts than the agar when the litmus was not used. There were fifty-seven comparisons in this series, the average plate counts of the gelatin being 38, while that of the agar was 60. The agar plates showed the higher count in forty-three of these fifty-seven sets. This indicates that the gelatin as a medium was not so efficient as the agar, irrespective of the use of litmus.

*Lactose agar, litmus lactose agar, lactose gelatin, and litmus lactose gelatin, compared*

In forty-two of the fifty-seven trials just mentioned, litmus lactose agar and litmus lactose gelatin were also used. The average plate counts were as follows:

| | Average plate count | | |
|---|---|---|---|
| Lactose agar | 62 | High count | 24 times |
| | | Low count | 1 time |
| Litmus lactose agar | 51 | High count | 6 times |
| | | Low count | 5 times |
| Lactose gelatin | 44 | High count | 10 times |
| | | Low count | 8 times |
| Litmus lactose gelatin | 28 | High count | 2 times |
| | | Low count | 28 times |

This shows that thruout this work the use of gelatin as a medium, and the use of litmus to differentiate between classes of bacteria, both tended to lower the plate count.

SUMMARY

1. An incubation temperature of 20° C. for seven days proved the best of any tried for growing bacteria from the ice cream on agar plates.

2. Of the ingredients used in ice cream, milk, cream, and condensed milk are by far the most prolific sources of bacteria. By effective pasteurization of these products before they enter the mix, ice cream can be made having a low bacteria content.

3. Aside from utensil contamination, there is usually an increase in the number of bacteria, as shown by the plate count in ice cream, resulting from the freezing process. This is probably due to the breaking up of clumps of organisms.

4. There is no radical change in the total number of bacteria in ice cream during storage. There seems, however, to be a tendency toward a slight decrease during the first two to four days, with a more noticeable increase and a corresponding decrease again between the fourth and the twenty-first day, after which time there is a very gradual falling off in numbers.

5. The groups of bacteria in ice cream as determined by litmus gelatin plates and litmus milk tubes do not change noticeably during storage. The acid formers predominate all thru the storage period, and many of them appear to be typical of the *Bacterium lactis acidi* group.

6. The greatest error in making counts of bacteria in ice cream by the plate method seems to be caused by uneven distribution in the final dilution water.

7. Agar plates gave higher counts than did gelatin plates, averaging three times as many bacteria as were found on the litmus gelatin plates. The use of litmus in both the agar and the gelatin plates decreased the counts somewhat.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# THE EFFECT OF MANGANESE COMPOUNDS ON SOILS AND PLANTS

E. P. DEATRICK

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# THE EFFECT OF MANGANESE COMPOUNDS ON SOILS AND PLANTS

# THE EFFECT OF MANGANESE COMPOUNDS ON SOILS AND PLANTS

E. P. Deatrick

Experimental evidence has shown that phosphorus, sulfur, potassium, calcium, magnesium, iron, carbon, hydrogen, oxygen, and nitrogen are essential to the normal growth and development of plants. Other elements, including manganese, are almost universally found in soils and plants, and this fact has led some investigators to assume that they perform important physiological functions. The weight of evidence, however, seems to indicate that the benefit following applications of a manganese compound to soil is due to its stimulative, indirect action either on the plant or on the soil, and manganese is therefore usually designated as a *catalytic fertilizer.*

The investigation here recorded was undertaken for the purpose of acquiring information regarding the specific effect of manganese compounds in increasing plant growth; in other words, to determine whether manganese is a direct plant stimulant, whether it increases the available food supply in the soil, or whether both these factors are operative. The direct stimulative or deleterious effect of a substance on plant growth may be determined by growing the plant to be studied in water cultures of a pure nutrient solution. When the same kind of plant is grown in soil to which the substance to be studied is added, the effect is usually very much modified. In the soil culture the action must be considered as the sum of the effects directly and indirectly on soil and plant.

## REVIEW OF LITERATURE

### *Experiments with water cultures*

The effects of manganese on plants have been studied by growing seedlings in distilled water alone, and in distilled water to which nutrient salts were added.

Working with the distilled water cultures, investigators have observed both stimulative and toxic effects. Loew and Sawa (1902–03)[1] found that in the presence of manganese in toxic quantities the leaves lose their

[1]Dates in parenthesis refer to *Literature cited*, page 399.

turgor and dry up, and no trace of new rootlets is apparent. In a solution containing 1000 parts per million of manganese sulfate, the leaves of barley plants faded to yellow and then turned brown. These investigators found also that barley became chlorotic and the roots turned brown in solutions containing only small quantities of manganese. McCool (1913) noted that a solution containing 15 parts per million of manganese in the form of chloride is injurious to field peas, and that a solution containing 30 parts per million prevents root growth entirely. Miss Brenchley (1914) found that manganese when present in strong concentrations exerts a toxic influence on higher plants.

On the other hand, several investigators have obtained plant stimulation in distilled water cultures containing small quantities of manganese. Micheels and De Heen (1906) obtained a pronounced stimulation in colloidal solutions of manganese. McCallum (1909) reported an acceleration of tuber formation when potatoes were treated with a solution of manganese chloride. Montemartini (1911), altho finding marked differences in the sensitiveness of plants, obtained increased growth with all plants used in his experiment. McCool (1913) found slight stimulation, as shown by length of the roots of pea seedlings, but the leaves showed no effect.

The effects of manganese in solutions containing nutrient salts are similar to those obtained with distilled water cultures, but experiments show that the nutrients greatly reduce the toxicity of the manganese. McCool (1913) found that this reduction of toxicity is proportional to the concentration of the nutrient salts.

According to Miss Brenchley (1914),

> the Rothamsted experiments supported Aso's work on the action of manganese sulphate on barley, concentrations of the salt above 1/100,000 having a retarding influence on the growth, the roots being coloured brown and the leaves also showing discolouration. At an early stage in growth the lower leaves of the plants receiving the most poison began to be flecked with brown spots.

A solution containing 1350 parts per million of nutrient salts and 770 parts per million of manganese in the form of sulfate, reduced the yield 31 per cent. A solution containing but 0.01 of this amount of manganese developed brown roots after four weeks and reduced the yield 3 per cent.

In lower concentrations manganese was decidedly stimulative. Aso (1902–03) found that manganese stimulated the growth of a number of plants. The solutions which he used contained 0.5 per cent of nutrient

salts and 0.02 per cent of manganese sulfate in one series, and 0.05 per cent of nutrient salts and 0.002 per cent of manganese sulfate in the other series.

Tottingham and Beck (1916) reported increased yields of wheat grown in nutrient solutions containing small quantities of manganese chloride.

Various views are held regarding the cause of the stimulation on the one hand and of the toxicity on the other. Loew and Sawa (1902–03) suggest that the stimulation by manganese is related to the oxidation of toxic substances within the plant leaf. They assert that certain noxious by-products are formed in the leaf, and that in reality sunlight retards growth. They state: "It is in the absence of light that growth proceeds and the products of the sun's work are chiefly consumed." Protoplasm oxidizes the carbohydrates formed, while the noxious by-products, probably members of the benzene group, are oxidized by enzymes, whose action is increased by the presence of manganese.

Many investigators find that the action of enzymes is in some way related to the presence of manganese. Kastle (1910) writes at length on manganese in its relation to the oxidizing ferments. It has been shown by Bertrand, he states, that the oxidizing power of laccase (from lucerne) is associated with the manganese content. He regards this element as the co-ferment, or activator, of laccase, just as hydrochloric acid is the co-ferment of pepsin. The oxidation of organic compounds, such as hydroquinon, by the oxygen of the air, is accelerated by the presence of manganese and varies with the form of the salt, being greater with the salts of the organic acids. These salts are "most easily hydrolyzable"; thus,

$$R''\mathrm{Mn} + \mathrm{HOH} = R''\mathrm{H_2} + \mathrm{MnO}.$$

The manganous oxide formed is "spontaneously oxidizable." In this oxidation, "molecular oxygen is split into two atoms, one of which combines with the manganous oxide to form the peroxide, the other going to oxidize the hydroquinon"; thus,

$$\mathrm{MnO} + \mathrm{O_2} = \mathrm{MnO_2} + \mathrm{O}, \text{ and}$$
$$\mathrm{C_6H_4\,(OH)_2} + \mathrm{O} = \mathrm{C_6H_4O_2} + \mathrm{HOH}.$$

In the presence of an acid, $R''\mathrm{H_2}$ is unstable and is capable of oxidizing more hydroquinon. Thus the manganese salt is regenerated. "According to this conception the manganese would be the really active element

of the oxidase, so far as the activation and transfer of oxygen is concerned, whereas the acid albuminoid radicle would impart to the ferment its other properties, such as its conduct toward heat, solubility, etc."

Manganese has been found to activate animal ferments. Considerable work has been done on the oxidizing power of colloidal solutions of manganese, which are described by Kastle as *artificial ferments.*

The reports of numerous investigators indicate that a relation exists between the presence of manganese and the production of chlorophyll. Van Dam (1907) states that seeds soaked in a solution of manganese sulfate yield plants which develop greener leaves than normally. Jadin and Astruc (1912) report that manganese constantly occurs in the ash of plants and that the chlorophyll-bearing parts contain the greatest proportion of this element. Mameli (1912) found that chlorophyll is produced in some of the lower plants only when manganese is added to the nutrient media. Pugliese (1913) states that there is an optimum ratio for iron and manganese, which he gives as 1:2.5. Mazé (1914) has described a special type of chlorosis due to the lack of manganese; a large amount in the plant also causes chlorosis. Gile (1916) is of the opinion that " manganese chlorosis may be due in part to a deficiency of iron in the plant, induced by the action of manganese in the plant or in the soil, and in part to a direct toxic action of the manganese." Johnson (1917) finds that the toxic effect of manganese on pineapples appears to be " due to a depression in the assimilation of iron," and has worked out a commercially successful method of counteracting the toxic effect by supplying iron thru the leaves.

*Experiments with soil cultures*

A large number of experiments are reported in which manganese salts have been applied to soil as a fertilizer. The results are somewhat contradictory.

Von Feilitzen (1907) found that manganese sulfate did not increase the yield of oats perceptibly. Pfeiffer and Blanck (1912), after experimenting with various salts and plants, decided that their results were not conclusive. They state that, while increased yields were occasionally obtained, the salts of manganese should not be recommended for general use as a fertilizer. This opinion is held also by Sullivan and Robinson (1913), who advised that manganese should not be used " in any way

other than in experimentation and as a fertilizer complementary to the usual chemical fertilizers." Masoni (1916) experimented with several manganese salts. Altho the chloride and the sulfate seemed to give a certain advantage, he believed the results were too small to indicate definitely the specific effect on the growth of the plants tested. Ehrenberg and Schultze (1917) state that experiments covering several years show that under many sorts of conditions neither a favoring nor an inhibitory action of manganese compounds on the growth of plants is demonstrable. At the Woburn station, however, Voelcker (1904) observed that manganese iodide, applied at the rate of 50 pounds to the acre, was very toxic to the growth of barley.

On the other hand, some surprising results have been obtained from the use of manganese salts. Javillier (1908) states that comparatively small quantities of this element have been sufficient to increase the yields of certain crops from 25 to 50 per cent. He believes there is no doubt that manganese compounds, particularly the sulfate, may be used advantageously as a complementary manure. Loew and Honda (1904–05) report an increase of 50 per cent in *Cryptomeria japonica* from fertilizing with manganese sulfate. With the use of the same salt Ray and Pradier (1909) were able to increase the yield of apricots 23 per cent. Bartmann (1910) cites Marre as having secured an increase of 60 per cent in some crops. Numerous other investigators have reported data indicating that manganese is a fertilizer of decided value.

A number of investigators, including Nagaoka (1906–08), and Skinner and his co-workers (1914, 1916), report data which are apparently contradictory. Nagaoka (1906–08) reported that in 1902 manganese sulfate applied at the rate of 70 pounds to the acre, increased the yield of rice 37 per cent; the following year the residual effect was considerable; in 1904 the season was "exceptionally favorable," but the treated plats again surpassed the checks; in 1905 the experiment was repeated, but that year the yield was greatly decreased. Skinner and Sullivan (1914) reported their work on the action of manganese in soils; they found that the growth of wheat was increased when various salts were added to a soil described as an *unproductive sandy loam*, while on a *productive loam* the salts had no stimulating effect.

Further experiments were reported by Skinner and Reid (1916), who state that "in a six-years field test of manganese sulphate used at the

rate of 50 pounds per acre on an acid silty clay loam, its effect each year was not beneficial to the crops grown." During the following years of experimentation the yields of the crops were increased. The soil had been found to be very acid, and large quantities of calcium carbonate were applied.

It appears that the reaction of the soil is a determining factor in the action of manganese. Nagaoka (1906–08) notes that the soil increases in acidity with the continued application of manganese sulfate. Rousset (1909) cites Malpeaux as securing contradictory results with both the sulfate and the chloride of manganese, but favorable results with the carbonate and the oxide applied in combination with marl.

Some results have been obtained, however, which point to a decreased stimulation when manganese is applied with some form of calcium. According to Uchiyama (1907), " A manurial mixture of a nearly neutral reaction, exerts the best effect. Manures of decisive alkaline or acidic nature on the other hand are not so favorable, since the former interferes with the effect of the manganese salt, while the latter are not suitable for the growth of most plants." Chittenden (1915–16) observed the same effect; he states that in two out of three cases manganese sulfate alone increased the yield, while the addition of lime to the manganese sulfate decreased the yield.

Many of the apparently inconsistent reports are explainable when complete data regarding the experiment are available. Some of the applications are too low. Others, as that of Crochetelle (1913), who applied an excessive amount (2000 pounds to the acre) of manganese sulfate to a " calcareous clay," are high yet stimulative.

References to the change which manganese compounds may undergo when added to soils are numerous. Nottin (1912) found that manganese is adsorbed like potassium or ammonia, and is precipitated by calcium carbonate and organic matter; the demanganization of water by calcium carbonate, and the precipitation of manganese found in dolomitized limestones, indicate that, in alkaline soils at least, the soluble salts of manganese are changed to oxides. In the soil solution, manganese probably occurs in the form of the bicarbonate, as Vincent (1916) concludes. Regarding solubility, Masoni (1916) states that the organic acids are particularly active in dissolving manganese. He claims that the behavior of the carbonates, sulfates, and oxides of manganese may be explained as phenomena of hydrolysis and of successive oxidation and reduction.

According to Schreiner, Sullivan, and Reid (1910:37), "soils may have practically the same amount of manganese and still vary greatly in oxidizing power, so oxidation in soils, if due to manganese, depends on the nature of the manganese as much as on the amount." The salts of manganese added to soils which were low in this element and had "very little oxidizing power," did not increase their power to oxidize aloin. Experiments to learn the effect on oxidation of the addition of hydroxy acids and salts to manganese compounds in the soil, led these authors to state (page 56 of reference cited): "This oxidation appears to be mainly nonenzymotic, the result of interaction between inorganic constituents and certain types of organic matter. It may also be brought about by organic matter in a state of autoxidation and by inorganic oxygen carriers, such as manganese and iron. Both processes activate oxygen."

According to Sullivan and Reid (1912:28), "That the catalytic power of the soil is correlated to some degree with the manganese content of the soil is evident." A comparison of soils of varying manganese content, and the failure of the addition of manganese salts to increase the catalytic power of soils that were poor catalyzers even tho the content of manganese was high, led these investigators to state that factors other than the "total amount of manganese must be the determinants." They suggest that either the nature of the manganese compound or the nature of the associated organic matter is more important than the amount of manganese.

### *Experiments with soil fungi and bacteria*

Altho the experimentation is meager, the weight of evidence supports the conclusions of Bertrand (1909) that manganese stimulates the growth of fungi. Loew and Sawa (1902–03), however, found no stimulation, and they have written at length on the difference of the behavior of manganese on the growth of phanerogams.

Kelley (1912) concluded that nitrification took place more rapidly in the soil high in manganese, while ammonification was about equal in soils of either high or low manganese content. Leoncini (1910) and Montanari (1914) have found that manganese increases the activity of nitrifying bacteria.

Brown (Brown and Minges, 1916) applied various salts of manganese to soil cultures, and concluded from his data that "if manganese salts in small quantities increase crop yields on a soil, that increase may be

due in part at least to a beneficial effect on ammonification and nitrification." If, on the other hand, the salts " restrict crop growth, that restriction may be due in part to a depression of bacterial activity."

Greaves (1916) has recently published his results. He states that with the possible exception of the chloride, all the manganese salts tested were strong stimulants to the ammonifying organisms of the soil. At maximum stimulation, 25 per cent more ammonia accumulated than in the normal soil.

Olaru (1915) states that the nitrogen-fixing power of bacteria from legumes is greatly increased by manganese. Gregario (1916) finds that mannitol bouillon containing 60 parts per million of manganese in the form of the chloride and inoculated with *Bacillus radicicola* fixes three times as much nitrogen as do the checks; a concentration of 200 parts per million retards the fixation. Furthermore, he finds that *Clostridium pasteurianum,* which normally is not a free fixer, becomes capable of fixing nitrogen in the presence of manganese. Similar results have been obtained with *Azotobacter chroococcum.*

*Summary*

Much of the evidence in the foregoing reports is contradictory. The results would be more intelligible if complete data regarding the experiments were given. The applications of manganese salts to soils have been made without any apparent consideration of the type of soil. Such factors as soil type, the presence of calcium, and the crop to be grown, are factors that determine the action of a given application. Large applications on a sandy loam are detrimental, while the same applications on a clay loam or on a soil high in calcium would in all probability be stimulative.

The rôle of calcium seems to be a complex one. If the manganese were stimulative in the soluble form, the addition of calcium would precipitate the manganese and prevent the stimulation. If, on the other hand, the manganese were present in such concentration as to be toxic, the addition of calcium would be beneficial, not only by causing precipitation of the manganese but also by increasing the oxidizing power of the soil by such precipitation.

Altho the evidence is in many respects inconclusive, the following statements seem to be justified by this review:

1. Manganese is universally distributed in small quantities in soils and plants.

2. The majority of experiments indicate that, as Miss Brenchley (1914) states, "manganese exerts a toxic influence upon the higher plants, if it is presented in high concentration, but, in the absence of great excess of the manganese compounds, the poisoning effect is overshadowed by a definite stimulation."

3. The toxicity of manganese is reduced by nutrient solutions and by soil.

4. Manganese compounds have been associated with the catalytic power of soils and with the oxidizing power of soils and plants. Comparatively large yields have been obtained with manganese fertilization under neutral or alkaline soil conditions, and the yields have been correlated with the oxidizing power of the soil. The stimulation of plants has in part been explained as due to increased activity in the metabolic processes within the leaf.

5. A stimulation of the ammonification and nitrification in soils has also been reported.

## EXPERIMENTAL WORK

### *Scope of present study*

In order to test the effect of manganese salts on the growth of plants, the weight of wheat seedlings grown in manganese solutions of varying concentrations (both in the presence and in the absence of nutrient salts) was compared with the weight of plants grown in cultures containing no manganese. The concentrations producing stimulation were then used as a basis for the applications in the experimental work conducted to test the manurial value of manganese when applied to soils. Dunkirk silt loam was treated with various manganese salts and planted with wheat. An attempt to explain the results obtained led to a study of the oxidizing, ammonifying, and nitrifying powers of soils treated with salts of manganese.

### *Effect of manganese compounds on wheat seedlings grown in water cultures*

Wheat seedlings (Jones' Paris Prize 106–43) from seeds germinated in running tap water were allowed to attain a growth of about eight centimeters, and were then transferred to culture containers. These were salt-mouth bottles of a capacity of 250 cubic centimeters, fitted with four-holed corks and wrapped in black paper. Each series was set up

in quadruple and was run for a period of two or four weeks. The nutrient solutions were made up from the following formulae:

| | | |
|---|---|---|
| Salt 1. Calcium nitrate | 27 | grams |
| Salt 2. Magnesium sulfate | 6 | grams |
| Salt 3. Potassium phosphate (monobasic) | 15 | grams |
| Salt 4. Ferric sulfate | 0.5 | gram |
| Salt 5. Potassium chloride | 7.5 | grams |

Salts 1 and 5 were dissolved together in 3 liters of water; salt 2 was dissolved in $1\frac{1}{2}$ liters, as was also salt 4, and both of these were mixed with salts 1 and 5. To the mixture was then added salt 3, after it had been dissolved in 3 liters of water. The total quantity was then increased to 10 liters by adding 1 liter of water. This solution contains 4656 parts per million of salts.

The wheat seedlings were placed in cultures containing 10, 20, 100, 200, 400, and 1000 parts per million of manganese in the form of manganese sulfate, and were harvested after remaining in the greenhouse for four weeks. The results are given in table 1:

TABLE 1. WHEAT SEEDLINGS (ENDOSPERMS NOT REMOVED) GROWN IN SOLUTIONS OF MANGANESE SULFATE. NO NUTRIENTS PRESENT

| Parts per million of manganese | Length (in centimeters) | | Weight of four plants (in grams) | | Total dry weight | Relative weights |
|---|---|---|---|---|---|---|
| | Leaves | Roots | Leaves | Roots | | |
| 0 | 11.7 | 18.2 | .0784 | .0514 | .1298 | 100 |
| 10 | 10.6 | 10.3 | .0940 | .0460 | .1400 | 108 |
| 20 | 11.5 | 5.6 | .0967 | .0319 | .1286 | 99 |
| 100 | 10.6 | 4.2 | .0658 | .0211 | .0869 | 67 |
| 200 | 12.4 | 4.6 | .0873 | .0163 | .1036 | 80 |
| 400 | 10.9 | 3.7 | .0770 | .0222 | .0992 | 76 |
| 1000 | 9.8 | 3.8 | .0641 | .0171 | .0812 | 63 |

As shown in table 1, solutions of manganese sulfate containing no nutrients were found to be toxic. All the manganese cultures, at the termination of the experiment, might be characterized as dead or dying. There was no great increase in growth, if any increase at all, even in the lowest concentration. The total dry matter was reduced in all cases except with a concentration of ten parts per million. The first symptom of the toxicity of manganese is the yellowing of the tips of the lower leaves.

Then bleaching occurs in small patches, which redden, dry, and turn brown. The intensity of this chlorotic condition decreases with the decrease in the concentration of the manganese. The roots of the plants grown in concentrations of 1000 parts per million turned brown in spots, especially at the tips, within four days. This browning occurred on the roots of all the plants except the checks, the length of time before the browning appeared being proportional to the concentration of the manganese.

The toxic effect was not so great in cultures of manganese sulfate containing nutrient salts (4656 parts per million) as in pure solutions, as is shown in table 2:

TABLE 2. MANGANESE SULFATE ADDED TO NUTRIENT SOLUTIONS CONTAINING 4656 PARTS PER MILLION OF NUTRIENT SALTS

| Parts per million of manganese | Length (in centimeters) | | Weight of four plants (in grams) | | Total dry weight | Relative weights |
|---|---|---|---|---|---|---|
| | Leaves | Roots | Leaves | Roots | | |
| 0 | 19.4 | 12.0 | 1713 | .0742 | .2455 | 100 |
| 10 | 17.8 | 15.4 | .2951 | .2033 | .4984 | 203 |
| 20 | 19.2 | 15.6 | .2668 | .1781 | .4449 | 181 |
| 100 | 21.2 | 14.0 | .2383 | .1294 | .3677 | 150 |
| 200 | 20.5 | 12.8 | .2250 | .1052 | .3302 | 135 |
| 400 | 20.7 | 9.3 | .2020 | .0780 | .2800 | 114 |
| 1000 | 16.0 | 5.9 | .1581 | .0459 | .2040 | 83 |

This demonstrates the ameliorating effect of the nutrient salts in overcoming or reducing the toxicity of a plant poison. At 1000 parts per million the total dry matter was reduced, but it equaled the check at 400 parts per million and increased with a decrease in the concentration of the manganese. The yellowing of the tips of the leaves at 1000 parts per million commenced in nine days. The browning of the roots was not observed in any of the cultures except those of greatest manganese content.

A second series of cultures was run in which the chloride, the carbonate, and the dioxide of manganese were used in addition to the sulfate. The seedlings of the first series, reported as having grown in solutions containing no nutrient salts, were in reality not grown in the absence of other elements. That the effect of the storage food in the endosperms is a factor in work of this nature, is suggested by McCool (1913), who states:

> Pea seedlings [cotyledons not removed] that have been grown for ten days in distilled water, tap water, and full nutrient solution, respectively, are much more resistant to the

poisonous influence of manganese than those that are transferred from germinating pans and placed immediately in solutions of manganese. The nature of the medium used in this preliminary treatment — that is, whether distilled water, tap water, or full nutrient solution — has no visible effect on the resisting power of the plants."

The seeds in this second series, consequently, were germinated as before, but when the seedlings were about eight centimeters high the endosperms were pinched off. This was done to eliminate as much as possible the influence of the storage food. The concentration of the nutrient solution was but one-fifth of that used in the previous series of cultures.

The average dry weight of the wheat seedlings at the time of setting up the cultures was determined, so that the effect of the manganese solutions might be the more accurately ascertained. The results are given in tables 3 and 4:

TABLE 3. WHEAT SEEDLINGS (ENDOSPERMS REMOVED) GROWN IN SOLUTIONS OF MANGANESE SALTS. NO NUTRIENTS PRESENT

| Parts per million of manganese | Average dry weight (grams) | Increase or decrease in weight during the two weeks (grams) | Relative increase or decrease in weights |
|---|---|---|---|
| 0 | .0319 | .0025 | 100 |
| **Manganese sulfate** | | | |
| 1 | .0336 | .0042 | 168 |
| 5 | .0304 | .0010 | 40 |
| 10 | .0298 | .0004 | 16 |
| 100 | .0309 | .0015 | 60 |
| 1000 | .0258 | —.0036 | —144 |
| **Manganese chloride** | | | |
| 1 | .0352 | .0058 | 232 |
| 5 | .0342 | .0048 | 192 |
| 10 | .0332 | .0038 | 152 |
| 100 | .0309 | .0015 | 60 |
| 1000 | .0252 | —.0042 | —168 |
| **Manganese carbonate** | | | |
| 1 | .0322 | .0028 | 112 |
| 5 | .0350 | .0056 | 224 |
| 10 | .0297 | .0003 | 12 |
| 100 | .0349 | .0055 | 220 |

TABLE 4. MANGANESE SALTS ADDED TO NUTRIENT SOLUTIONS CONTAINING 961 PARTS PER MILLION OF NUTRIENT SALTS

| Parts per million of manganese | Average dry weight (grams) | Increase in weight during the two weeks (grams) | Relative increase in weights |
|---|---|---|---|
| 0 | 0367 | .0073 | 100 |
| **Manganese sulfate** | | | |
| 1 | .0392 | .0098 | 134 |
| 5 | .0404 | .0110 | 151 |
| 10 | .0423 | .0129 | 177 |
| 100 | .0400 | .0106 | 145 |
| 1000 | .0368 | .0066 | 90 |
| **Manganese chloride** | | | |
| 1 | .0385 | .0091 | 125 |
| 5 | .0419 | .0125 | 171 |
| 10 | .0395 | .0101 | 138 |
| 100 | .0387 | .0093 | 127 |
| 1000 | .0320 | .0026 | 36 |
| **Manganese carbonate** | | | |
| 1 | .0367 | .0073 | 100 |
| 5 | .0376 | .0082 | 112 |
| 10 | .0387 | .0093 | 127 |
| 50 | .0455 | .0161 | 220 |

It will be noticed that by this procedure it has been possible to show an actual decrease in the weight of the seedlings grown in the solutions of highest concentrations of the sulfate and the chloride.

An examination of tables 3 and 4, giving the results of this series of experiments, shows that these results agree in general with those of the first series; that is, as the concentration of the manganese decreases, the total dry weight increases. The figures show clearly the greater toxic effect of the manganese in the absence of the endosperm. The results here reported agree closely with those of Miss Brenchley (1914).

*Effect of manganese compounds on wheat grown in soil*

The determination of the effect of a given factor when added to the soil is complex. The effect of this factor on the growth of plants is but

an indication of its resultant effect on the various activities in a complex medium. It was therefore deemed advisable to determine, in the first place, whether the addition of manganese sulfate to soil cultures inhibits its power to function as in the case of water cultures. Consequently, wheat was grown on soil to which manganese sulfate had been added in varying amounts.

In this, as well as in other soil experiments, the soil used was Dunkirk silt loam, obtained near the experimental plats of Caldwell Field. The results of the chemical and mechanical analyses are given in tables 5 and 6, respectively:

TABLE 5. CHEMICAL (BULK) ANALYSIS OF DUNKIRK SILT LOAM

| Constituent determined | Surface 1 to 12 inches (per cent) | Subsoil 12 to 24 inches (per cent) |
|---|---|---|
| Nitrogen (N) | 0.186 | 0.082 |
| Organic carbon (C) | 1.670 | 0.440 |
| Carbon dioxide ($CO_2$) | Trace | 0.260 |
| Calcium oxide (CaO) | 0.430 | 0.830 |
| Magnesium oxide (MgO) | 0.450 | 0.690 |
| Potassium oxide ($K_2O$) | 1.740 | 2.110 |
| Sodium oxide ($Na_2O$) | 1.090 | 1.280 |
| Phosphoric anhydride ($P_2O_5$) | 0.123 | 0.126 |
| Manganese oxide ($Mn_3O_4$) | 0 | 0 |

TABLE 6. MECHANICAL ANALYSIS OF DUNKIRK SILT LOAM

| | Per cent |
|---|---|
| Fine gravel | 0.5 |
| Coarse sand | 0.8 |
| Medium sand | 0.6 |
| Fine sand | 2.7 |
| Very fine sand | 9.5 |
| Silt | 67.3 |
| Clay | 18.6 |

The soil was procured in quantity, was allowed to partially dry out in the air, and was then passed thru a 2-millimeter sieve. After treatment with manganese sulfate the soil was placed in small wire baskets, 350

grams to a basket. The baskets were paraffined and a sand mulch was placed on the surface. Six baskets of each treatment were set up, four of which were planted with wheat seedlings about 10 centimeters high. There were four seedlings in each basket. The baskets were carried to the greenhouse, where they remained for a period of three months. During that period they received such applications of distilled water, from time to time, as would bring the soil up to the original moisture content of 25 per cent (dry basis). On May 3, 1916, the crop was harvested, and the plants were dried, weighed, and analyzed for manganese. The results are given in table 7:

TABLE 7. WHEAT GROWN FOR THREE MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE

| Parts per million of manganese added | Average weight of seedlings in each culture (grams) | Relative weights |
|---|---|---|
| 0 | 2.70 | 100 |
| 10 | 3.25 | 120 |
| 50 | 2.80 | 104 |
| 100 | 1.94 | 72 |
| 1000 | 2.05 | 76 |

An examination of the relative weights shows that the manganese is at least not prevented entirely from stimulating plant growth when it is added to soil. The stimulation at 10 parts per million was appreciable.

Another set of cultures was arranged on December 12, 1916. Two kilograms of air-dry soil, to which the various quantities of manganese sulfate were added, was placed in wire baskets. These baskets then received a coating of paraffin and a sand mulch. Seven of the baskets received an application of calcium carbonate at the rate of 20,000 parts of CaO per million of soil. The soil was seeded to wheat and the moisture content was raised to 25 per cent (dry basis), where it was kept by the addition of distilled water from time to time. One month later the seedlings were thinned to five to a basket, and these were allowed to grow for seven and

one-half months. The crop was harvested on July 3, 1917. The yields obtained are recorded in tables 8 and 9:

TABLE 8. WHEAT GROWN FOR SEVEN AND ONE-HALF MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE

| Parts per million of manganese added | Weight of straw | | Weight of grain | |
|---|---|---|---|---|
| | Average (grams) | Relative | Average (grams) | Relative |
| 0 | 5.6 | 100 | 2.0 | 100 |
| 10 | 5.0 | 89 | 4.0 | 200 |
| 25 | 5.7 | 102 | 4.1 | 205 |
| 50 | 3.5 | 62 | 2.3 | 115 |

TABLE 9. WHEAT GROWN FOR SEVEN AND ONE-HALF MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE

| Parts per million of manganese added | Weight of straw | | Weight of grain | |
|---|---|---|---|---|
| | Average (grams) | Relative | Average (grams) | Relative |
| 0 | 1.7 | 100 | 1.7 | 100 |
| 10 | 4.5 | 265 | 2.0 | 118 |
| 25 | 4.9 | 288 | 1.8 | 106 |
| 50 | 5.0 | 294 | 2.1 | 123 |

The effect of the manganese in these cultures is not apparent when the yields are considered. Practically all the yields of the soil treated with manganese are somewhat higher than those treated with calcium. The yield for the calcium carbonate check is strikingly low, for which no reason can be assigned by the writer. Greater differences, however, than those that appear in the data of table 9, were noted at an earlier stage of growth. It was observed that a majority of the manganese plants headed before the calcium-manganese plants did. In this respect it would seem that the calcium had interfered with the action of the manganese.

Other investigators have stated that the effect of manganese on yield is not marked. While Bertrand (1909) notes that the favorable results of manganese are not apparent until harvest time, Miss Brenchley (1914) states that there is a retarding effect on the ripening of the grain but not on the yield. Takeuchi (1909–13) reports that the control plants of flax were behind the manganese plants in growth and flowering. Aso (1904–05) found that rice treated with manganese flowered four days earlier than did the checks. Salomone (1907) states that the stimulation of the vegetative portion of plants is greater than that of the grain. Comparison of the data in tables 7 and 8 shows that greater differences in the yields were obtained when the plants were harvested before they matured.

### *Manganese content of yellow leaves*

Several investigators have reported that the yellow leaves of manganese plants contain more manganese than do the green leaves. The leaves of the plants grown on soil treated with manganese sulfate (page 385) were analyzed for their manganese content by the colorimetric method described in Bulletin 31 of the United States Bureau of Soils. The results are given in table 10:

TABLE 10. ANALYSES OF LEAVES OF WHEAT GROWN ON SOIL TREATED WITH MANGANESE SULFATE

| Parts per million of manganese added | Manganese (in parts per million grams of dry matter) in | | |
|---|---|---|---|
| | Green leaves | Yellow leaves | Medium yellow leaves |
| 0 | Trace | Trace | Trace |
| 10 | Trace | Trace | Trace |
| 50 | Trace | 3.8 | 1.22 |
| 100 | 1.15 | 7.25 | 3.37 |
| 1000 | 1.95 | 11.25 | 3.12 |

If Aso (1902–03) is correct in stating that the colorimetric tests for the oxidizing enzymes showed that "the yellowish leaves of the manganese plants gave reactions of higher intensity than the green leaves of the control plants," it seems that the intensity of these enzymes is proportional to

the manganese content of the leaves. Woods (1899) states: "It has long been known that chlorophyll could be readily converted by oxidation, into a yellow coloring matter, xanthophyll." While a moderate stimulation of the oxidizing power of the plant juices may result beneficially, an excessive stimulation may result in the oxidation of the chlorophyll.

*Relation of manganese to the oxidizing power of soils*

In some cases the lack of fertility in a soil has been shown to be due to the presence of certain organic substances injurious to plant growth. Schreiner and Shorey (1909) found that when such soils are well aërated they become productive. Schreiner, Sullivan, and Reid (1910:44) state that the addition of manganese to soils promotes "the most active oxidation," and "by its strong oxidizing power . . . . . would render the injurious material in the soil harmless or even beneficial and by the oxidation of inert or rather stable organic matter might cause" a liberation of plant food. A brief study of the effect of manganese salts on the oxidizing power of soils has therefore been made by the writer.

Portions of Dunkirk silt loam were sprayed with solutions of manganese chloride, manganese sulfate, potassium permanganate and suspensions of manganese carbonate, and manganese dioxide, in quantities such that the manganese added was in the proportion of 10, 100, and 1000 parts of manganese per million of dry soil. It was thought that by spraying the soil a more uniform distribution of the manganese could be obtained. Consequently the calculated amounts of the salts were added to sufficient water to bring the soil to 25 per cent moisture content (dry basis). The spraying was done with a simple atomizer, made with two pieces of glass tubing of different bore and a wide-mouth bottle. It was found that the physical condition of the soil was very good when the water was added in this way. A determination showed that the moisture lost in the form of mist and evaporation during the treatment was negligible. The soils were stored in glass quart jars for about seven months.

To test the oxidation in the soil, 50 cubic centimeters of the following solution was added to 10 grams of the air-dried soil in a centrifuge tube:

10 grams aloin
200 cubic centimeters N/10 HCL
790 cubic centimeters distilled water

The tube was shaken for exactly one-half minute and was then placed in the centrifuge, which was started one minute after the solution was added. At the end of two minutes the electric current was turned off the centrifuge, and the speed was allowed to decrease gradually while a second test was started. Five minutes after the aloin was added in the first test, a portion of the supernatant liquid was poured into a colorimeter tube and the depth of color was compared with that of a standard.

This method will be found to differ considerably from that of Schreiner, Sullivan, and Reid (1910). The oxidation in the soils reported was so great that it was found necessary to use the method already described. The difference between the two methods is indicated by the following:

| | Schreiner, Sullivan, and Reid | Deatrick |
|---|---|---|
| Time of test | 2 to 3 hours | 5 minutes |
| Concentration of aloin solution | 0.125 per cent | 1.0 per cent |
| Flocculating agent | $C_2H_5OH$ | HCL |

The standard used in the writer's experiments was a solution of aloin which had been completely oxidized with either manganese dioxide or nitric acid. The results were calculated on the basis of the oxidation in the untreated soil as 100.

The oxidation of phenolphthalin (made by reducing phenolphthalein with zinc dust and sodium hydroxide) was also used as a means of testing the oxidation in soils. The data are given in table 11. These figures indicate definitely that the addition of manganese salts to soils increases the power to oxidize organic matter such as aloin and phenolphthalin. It appears that the salts which are the most effective are the permanganate, the chloride, and the sulfate.

While the treatment with manganese dioxide seems to have interfered slightly with oxidation, it has been observed that soils treated with precipitated manganese oxides, instead of the pulverized pyrolusite, oxidize aloin readily. The oxidation in the air-dry soil from the field was very weak. The increase due to the moisture treatment alone is very noticeable. Since the soil contains no manganese, this is due to some other cause.

TABLE 11. OXIDATION IN DUNKIRK SILT LOAM TREATED WITH MANGANESE SALTS
(Tests made seven months after treatment)

| Parts per million of manganese added | Relative oxidation | |
|---|---|---|
| | Aloin | Phenolphthalin |
| 0 | 100 | 100 |
| **Potassium permanganate** | | |
| 10 | 101 | 100 |
| 100 | 136 | 120 |
| 1000 | 444 | 200 |
| **Manganese dioxide** | | |
| 10 | 93 | 100 |
| 100 | 94 | 100 |
| 1000 | 95 | 100 |
| **Manganese chloride** | | |
| 10 | 105 | 100 |
| 100 | 113 | 125 |
| 1000 | 171 | 167 |
| **Manganese carbonate** | | |
| 10 | 105 | 100 |
| 100 | 117 | 100 |
| 1000 | 128 | 142 |
| **Manganese sulfate** | | |
| 10 | 105 | 100 |
| 100 | 136 | 130 |
| 1000 | 233 | 172 |

### *Adsorption of manganese*

It had been noted that soil to which manganese salts were added developed a power to oxidize aloin in proportion to the length of time that the salt was in contact with the soil. In order to test this more accurately, portions of soil, the moisture content of which had been held at 25 per cent for seven months, were treated with solutions of manganese sulfate. The data, given in table 12, indicate that oxidation does not develop at once, but that it is greatest in the soil in which the manganese has been present for the longest time.

TABLE 12. EFFECT OF DURATION OF CONTACT OF SOIL WITH MANGANESE SULFATE, ON THE OXIDIZING POWER OF THE SOIL

| Parts per million of manganese added | Date when manganese was added | Date when oxidation was determined | Relative oxidation |
|---|---|---|---|
| 10 | April 3, 1916 | November 8, 1916 | 100 |
| 10 | November 8, 1916 | November 8, 1916 | 100 |
| 1000 | April 3, 1916 | November 8, 1916 | 185 |
| 1000 | November 8, 1916 | November 8, 1916 | 112 |

In order to test the adsorptive power for manganese, four percolation cylinders were filled with Dunkirk silt loam, a kilogram to each cylinder. The cylinders were labeled A, B, C, and D, respectively. To soils C and D calcium hydroxide was added at the rate of 10,000 parts of CaO per million of soil. Soils A and B were untreated. A solution of manganese sulfate containing 1000 parts per million of manganese was then percolated thru the soils after they had been saturated with distilled water. Each successive 100 cubic centimeters of the percolate was analyzed for manganese by the colorimetric method described in Bulletin 31 of the United States Bureau of Soils. The manganese content of the percolates, expressed in parts per million, is given in table 13:

TABLE 13. MANGANESE CONTENT OF MANGANESE SULFATE SOLUTION (1000 PARTS PER MILLION OF MANGANESE) PERCOLATED THRU DUNKIRK SILT LOAM

| Successive 100-cc. portions of percolate | Manganese content in parts per million | | | |
|---|---|---|---|---|
| | A | B | C | D |
| 1 | 0 | 0 | 0 | 0 |
| 2 | Trace | 111 | 0 | 0 |
| 4 | 62 | 286 | 0 | 0 |
| 6 | 500 | 400 | Trace | 0 |
| 8 | 625 | 417 | 62 | Trace |
| 10 | 715 | 455 | 154 | 92 |
| 12 | 715 | 500 | 218 | 167 |
| 14 | 715 | 525 | 256 | 143 |
| 16 | 715 | 555 | 357 | 222 |
| 18 | 770 | 475 | 357 | 91 |

The soils treated with calcium hydroxide precipitated more manganese than did the untreated soils. In the case of soil C, one liter of the solution was passed thru it before any appreciable amount of manganese appeared in the percolate. On air-drying these soils, C and D were found to have an intensive oxidizing power as compared with A and B.

Soils treated with 1000 parts per million of manganese in the form of pulverized pyrolusite were found not to have a strong oxidizing power. A solution of aloin, however, is rapidly oxidized when some of the pyrolusite is added to it. Colloidal manganese dioxide (from potassium permanganate and hydrochloric acid, purified by decantation) oxidizes aloin immediately. These phenomena, added to the fact that soils C and D developed the oxidizing power immediately in the presence of calcium, have led the writer to believe that the oxidation in soils due to manganese is due to the presence of manganese dioxide. In a solution of a manganese salt, manganic hydroxide is readily formed on the addition of an alkali. The formation of the oxide in soil to which a soluble manganese salt has been added, is directly proportional to the lime content, that is, the basicity of the soil. In the absence of an excess of an alkali form of calcium, the formation of the oxide of manganese is slower, for the stability of the soluble salts, as the sulfate and the chloride, is of course greatest in an acid solution. The salts of the weak acids, however, are not so stable, and when adsorption phenomena play a part, the salts are unstable even in neutral media. Thus, if pure, fine sand is treated with a solution of manganese citrate, this instability is soon demonstrated by the browning of the sand. This has been found to be the case with sand so treated and stored in a jar. On exposure to air, sand treated with the acetate and the citrate has developed a slight brown color.

Schreiner, Sullivan, and Reid (1910) apparently tested their soils immediately after adding the manganese salts. These soils were probably deficient in lime, and therefore the addition of manganese did not increase oxidation. The increase noted when hydroxy acids were added to these soils may have been due to the formation of the organic salt of manganese and the subsequent precipitation of the oxide from the less stable salt.

The formation of the dioxide, and the oxidation phenomena in soils as described, are analogous to the formation of calcium manganite (CaO.

$MnO_2$) and its use in the Weldon recovery process for the preparation of chlorine. The mixture of milk of lime and manganese chloride is termed *Weldon*, or *manganese, mud.*

*Oxidation by plant roots*

That roots of plants have an extracellular oxidizing power " may be demonstrated by the use of suitable chromogens," according to Schreiner and Reed (1909). In regard to their work on root oxidation in culture solutions containing alpha-naphthylamine, these investigators state (page 17 of reference cited) that " when the oxidation is performed by the growing roots of a plant, the oxynaphthylamine is deposited upon the surface of the roots in characteristic zones. . . . . The zone of primary meristematic cells immediately back of the root cap is marked by a distinct narrow band of color." The browning of the roots of wheat in solutions of manganese salts resembles the staining caused by the oxidation of alpha-naphthylamine.

The reports of investigators indicate that such browning is characteristic of plants other than wheat, when grown in manganese solutions. This browning has been reported as consisting of a deposit of manganese dioxide. As far as can be ascertained by the writer, no proof has been offered for this statement. That the dioxide is formed, however, is indicated by the following: The black deposit is insoluble in water but dissolves in hydrochloric acid. When this solution is evaporated and the residue is fused with an alkali carbonate on platinum foil, the characteristic green color of the alkali manganate is developed. Furthermore, the blackened roots are capable of liberating chlorine from a solution of a chloride and sulfuric acid. If the plants thrive long enough in the manganese solution, the whole root system becomes blackened.

In writing of the deposit of manganese dioxide, Miss Houtermans (1912) states that the blackening is probably the result of enzymotic processes. The browning is the result of the oxidation which occurs on the surface of the root. The fixed alkali hydroxides precipitate from solutions of manganese salts manganous hydroxide, white, which readily turns to brown manganic hydroxide in the air or in contact with other oxidizing agents. Since manganous hydroxide is formed in the solution of a manganese salt by hydrolysis, it seems that it is deposited on the roots, as such, and

is there oxidized to a higher oxide, as the insoluble brown deposit. Soon after the heavy deposition of the oxide, disintegration of the root occurs.

Schreiner and Reed (1909) conclude that "the process of oxidation by roots is largely, if not entirely, due to the activity of a peroxidase produced by the roots." That the deposit is not caused merely by the instability of the manganese solutions in the presence of organic matter is indicated by the absence of any blackening on pieces of string or wood placed in them. A definite relation has been established between stimulants of this oxidizing power and stimulants of growth. Schreiner, Sullivan, and Reid (1910:9) state that "oxidation by plant roots is a factor which has considerable agricultural interest, especially from the viewpoint that such oxidation is able to change the organic matter in the medium in which the plant is growing and that processes promoting oxidation play a large part in the best methods of soil cultivation."

The effect of manganese on the oxidizing power of the roots of wheat seedlings was therefore investigated. Seedlings were set up as before in nutrient solutions (931 parts per million of salts) and grown for two weeks. Portions of these solutions were then treated with small quantities of the aloin solution and allowed to stand for twenty-four hours, and a comparison was then made of their relative oxidation. The results appear in table 14:

TABLE 14. EFFECT OF MANGANESE SULFATE ON OXIDATION BY ROOTS

| Parts per million of manganese | Oxidation in solutions | |
|---|---|---|
| | With plants | Without plants |
| 0 | 100 | 0 |
| 1 | 184 | 0 |
| 5 | 191 | 0 |
| 10 | 181 | 0 |
| 50 | 244 | 0 |
| 100 | 250 | 0 |
| 1000 | 206 | 167 |

In every case the cultures in which plants had grown oxidized the aloin more than did those in which no plants were grown. In fact, the aloin was but faintly oxidized in the checks, and with the exception of the one containing the greatest quantity of manganese the degree of oxidation

was considered as zero. When phenolphthalin was used as an indicator similar results were obtained, altho some trouble was experienced with these solutions because of the carbon dioxide content.

The bluing of gum guaiac was also used as an indication of the oxidizing power of the roots. The reagent, which was poured on the surface of the cultures, followed the path of the roots where it was oxidized. The objection has been raised that due consideration was not given to the oxidizing power of the manganese sulfate. It was found that a solution of gum guaiac is oxidized immediately by a solution of manganese sulfate containing approximately 10,000 parts per million of manganese. A solution of 1000 parts per million, however, gave only a slight bluing after three hours. Immediate bluing was obtained by the roots of plants grown in the presence of 10 parts per million of manganese in the form of the sulfate, while the bluing by the roots of the check plants was slow and not so intense.

*Effect of manganese sulfate on soil bacteria*

Numerous investigators have reported that the activity of the lower forms of plant life is increased by the presence of manganese salts. In order to test this point, cultures were set up to determine the effect of manganese sulfate on the ammonification of dried blood and the nitrification of ammonium sulfate in soil. These cultures were prepared from a fresh stock of Dunkirk silt loam, which had been passed thru a two-millimeter sieve and which contained 12 per cent (dry basis) of water. Portions of the soil each weighing 112 grams were placed in eight-ounce salt-mouth bottles. When properly treated the cultures were placed on the laboratory desk and covered with a moist pad, made of cheesecloth and cotton, to prevent the evaporation of water. It was found that in this way a large number of cultures could be kept at a constant moisture content with the expenditure of a minimum amount of labor. The cultures were run in quadruplicate and were incubated at room temperature. Two days after the cultures were set up, the soil in each bottle was stirred so as to insure uniformity in the distribution of the salts added. At the end of the incubation period, the soil in each bottle was stirred with 475 cubic centimeters of distilled water for three minutes and then allowed to settle for twenty minutes, and the supernatant liquid was filtered thru a Pasteur-Chamberlain filter. Aliquot portions of the filtrate were then analyzed for ammonia and nitrates. The ammonia was deter-

mined by adding concentrated sodium hydroxide, distilling, and titrating the distillate with tenth-normal hydrochloric acid. The nitrates were determined by the phenol-disulfonic-acid method, using the Schreiner colorimeter to read the intensity of color.

*Ammonification.*— To the soil used for ammonification tests was first added 0.5 per cent of dried blood. The manganese sulfate was added after the soil had been weighed out and placed in the culture bottles. Sufficient water was used as the solvent of the manganese sulfate to bring the soil in each culture to a moisture content of 25 per cent (dry basis). The cultures were incubated for one week, at the end of which extracts and determinations were made as described above. The results are given in tables 15 and 16:

TABLE 15. EFFECT OF MANGANESE SULFATE ON AMMONIFICATION OF DRIED BLOOD IN DUNKIRK SILT LOAM

(Cultures incubated for seven days)

| Parts per million of manganese added | Nitrogen as ammonia, average of 4 cultures (milligrams) | Relative amounts |
|---|---|---|
| 0 | 34 | 100 |
| 10 | 47 | 138 |
| 20 | 53 | 156 |
| 30 | 47 | 138 |
| 50 | 54 | 159 |
| 70 | 58 | 170 |
| 100 | 67 | 197 |

TABLE 16. EFFECT OF MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE ON AMMONIFICATION OF DRIED BLOOD IN DUNKIRK SILT LOAM

(Cultures incubated for seven days)

| Parts per million of manganese added | Nitrogen as ammonia, average of 4 cultures (milligrams) | Relative amounts |
|---|---|---|
| 0 | 87 | 100 |
| 100 | 96 | 110 |
| 1000 | 109 | 125 |

The addition of manganese sulfate to the soil resulted in a positive stimulation in the ammonifying power. The addition of calcium carbonate resulted in a greater stimulation than that caused by the manganese alone. The stimulation of the manganese is not so great in alkaline soil as in soil deficient in calcium. This is as would be expected, for the solubility of the manganese is decreased.

*Nitrification.*— To the soil used for nitrification tests, 220 parts per million of nitrogen in the form of ammonium sulfate was added. The calculated quantities of solutions of manganese and ammonium sulfate were mixed, and were added to the soil in the culture bottles together with sufficient water to bring the soil to a moisture content of 25 per cent (dry basis). The cultures were incubated for four weeks. At the end of this time the extracts and determinations were made as described, and the results, expressed as parts of nitrates per million parts of dry soil, are given in tables 17 and 18. The experimental error of this deter-

TABLE 17. EFFECT OF MANGANESE SULFATE ON NITRIFICATION OF AMMONIUM SULFATE IN DUNKIRK SILT LOAM

(Cultures incubated for thirty days)

| Parts per million of manganese added | Nitrates, average of 4 cultures (parts per million of soil) | Relative amounts |
|---|---|---|
| 0 | 234 | 100 |
| 10 | 236 | 101 |
| 20 | 252 | 108 |
| 30 | 197 | 84 |
| 50 | 156 | 67 |
| 70 | 136 | 58 |
| 100 | 122 | 52 |

mination is large, and the data given in the tables indicate that manganese sulfate in low concentrations did not affect the nitrifying power of the soil. In soils containing larger amounts of manganese, however, the nitrification was checked.

TABLE 18. EFFECT OF MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE ON NITRIFICATION OF AMMONIUM SULFATE IN DUNKIRK SILT LOAM

(Cultures incubated for thirty days)

| Parts per million of manganese added | Nitrates, average of 4 cultures (parts per million of soil) | Relative amounts |
|---|---|---|
| 0 | 344 | 100 |
| 100 | 326 | 95 |
| 1000 | 273 | 79 |

## *Conclusions*

The experimental data here reported seem to justify the following conclusions:

1. Manganese salts added to water cultures affect the growth of wheat seedlings. The comparison of relative weights shows that when presented to the plant in high concentrations, both the sulfate and the chloride exert a toxic effect. In lower concentrations, manganese causes a marked stimulation.

2. The degree of toxicity is reduced by full nutrient solutions and the reduction is directly proportional to the concentration of the nutrient salts. Likewise, the food stored in the endosperms reduces the toxicity of the plant poison.

3. The toxic influence results in the browning of the roots and the bleaching of the leaves. The yellow leaves of the manganese plants contain more manganese than do the green ones.

4. Manganese salts added to soil form manganese dioxide in proportion to the basicity of the soil, and thus develop a power to oxidize organic matter as shown by the oxidation of aloin or phenolphthalin.

5. Manganese sulfate in water cultures stimulates the oxidizing power of the roots of wheat seedlings.

6. Low concentrations of manganese sulfate were found to stimulate the ammonification of dried blood in soil. The nitrification of ammonium sulfate was inhibited.

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AGRICULTURAL EXPERIMENT STATION

# THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS

WALLACE LARKIN CHANDLER

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# THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS

# THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS[1]

WALLACE LARKIN CHANDLER[2]

The present rapid development in America of industries which utilize large quantities of benzene or its derivatives in the manufacture of their products has greatly augmented the importance of the question of industrial poisoning. This is especially true of those industries in which nitrobenzene is used in some particular stage of a manufacturing process. Because of the pleasant odor and the retarded physiological action of nitrobenzene its toxic properties are not generally recognized, with the result that many workmen are constantly endangered by being either in actual contact with the liquid or exposed to its poisonous fumes. Furthermore, the physiological symptoms of nitrobenzene poisoning are not well understood, altho medical literature contains a large number of reports of such poisoning; and undoubtedly a large number of cases of industrial nitrobenzene-poisoning have been referred to other causes, the real cause having been obscured by the retarded and inconstant action of this chemical.

In the hope of obtaining more specific data regarding the physiological action of nitrobenzene, the initial experiments conducted by Dr. M. Dresbach and the writer on the investigation of nitrobenzene as a parasiticide (Chandler, 1917)[3] were continued. The present researches have resulted in findings which, it is hoped, may serve to make clear some of the factors regarding the action of nitrobenzene which hitherto have not been understood; for example, the cause of the "latent period," the reason for the inconstancy of certain symptoms, and the specific nervous centers involved. The work has also opened up new fields for investigation along the lines of neurology, physiology, and biochemistry.

The writer is indebted for advice and assistance to the following members of the faculty of Cornell University: Dr. M. Dresbach, of the Depart-

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[3] Dates in parenthesis refer to *Literature cited*, page 471.

ment of Physiology and Biochemistry; Dr. William A. Riley, of the Department of Entomology; Dr. E. M. Chamot, of the Department of Sanitary Chemistry and Toxicology; Dr. H. M. Kingery, of the Department of Histology; and Professor S. H. Gage, of the Department of Histology.

## INTRODUCTION

Nitrobenzene (mononitrobenzene, nitrobenzol, oil of mirbane, artificial oil of bitter almonds, and so forth), $C_6H_5NO_2$, is a clear, straw-colored, oily liquid boiling at 210.9° C. and crystallizing in needles at 5.7° C.[4] It has the odor of oil of bitter almonds, and when undiluted has a pungent, unpleasant taste. It is soluble in all parts of alcohol, in ether, chloroform, benzene, oils, and liquid fats, and to some extent in lipoids. It is but slightly soluble in water. It has a vapor pressure of but 1 millimeter of mercury at 53° C. It is combustible, burning in the open air with a sooty, yellowish flame, and is explosive when heated to high temperatures such as would be obtained by throwing it on red-hot iron. It was first made by Mitscherlich (1834). At present it is manufactured on a large scale by "adding one part of benzene to three parts of a mixture of nitric acid (sp. gr. 1.40) and sulphuric acid (sp. gr. 1.84), this mixture being made up of 40 parts of the former to 60 parts of the latter" (Weaver, 1917). It is used in the manufacture of explosives (indurite); in the manufacture of anilin, which is used extensively in the making of dyes; in perfuming soaps, lotions, pomades, and other toilet articles; as a solvent in the manufacture of shoe polish, floor wax, and the like; in the manufacture of flavoring extracts and certain liqueurs; and for flavoring confections. It was recommended and used with friction as a parasiticide as early as 1863,[5] and has recently been recommended as a fumigant for the extermination of the external parasites of domesticated animals (Moore, 1916).

The poisoning effects of nitrobenzene were noted as early as 1856. Since that time, numerous cases of fatal poisoning in man have been reported, and several experiments on animals have been conducted for the purpose of studying the poisonous action of the chemical.

[4] Determined experimentally. (See also Landolt, Börnstein, and Roth, 1912.)
[5] This recommendation stimulated investigations by Ollivier and Bergeron (1863) and by Guttmann (1866).

## REVIEW OF LITERATURE

According to Letheby (1865), the ancient Greeks were apparently familiar with a substance the physiological action of which is similar to that of nitrobenzene. He states as follows:

> It is said that Thrasyas, the father of botany, was so skilled in the preparation of drugs, that he knew how to compound a poison which would ..... kill by a lingering illness. Theophrastus speaks of this poison, and says its force could be so modified as to occasion death in two, three, or six months, or even at the end of a year or two years; and the writings of Plutarch, Tacitus, Quintilian and Livy are full of instances of what seem to be the same kind of slow and occult poisoning.

However, nitrobenzene itself was unknown to modern chemistry until its discovery by Mitscherlich in 1834.

Most of the literature relating to the toxic properties of nitrobenzene consists of clinical reports of accidental cases of poisoning, and, from the standpoint of obtaining data on the physiological action of the drug, is unreliable for the reason that important information regarding the patient's "normal" condition is entirely lacking. Also, in the few experiments recorded dealing with its physiological action on animals, the drug was administered in the liquid form by either intravenous injections or introduction into the stomach by means of a tube, and very seldom by vapor inhalation. However, a review of some of these cases, both clinical and experimental, may serve to help interpret the results of the present experiments. Short abstracts of a few of these are therefore given.

### CLINICAL CASES OF POISONING

Probably the most interesting clinical record is the case reported by Grafe and Homberger (1914) of a man who worked in a nitrobenzene factory filling containers with nitrobenzene. After working in this capacity for a period of fourteen days the man began to show symptoms of poisoning. These symptoms were a blue-gray color of the skin, headache, backache, stomach-ache, and vomiting. He continued to work for a few days after the onset of the symptoms. On Friday, October 27, 1905, he filled a double number of containers (ordinarily he handled 1600 liters), and on Saturday it was with difficulty that he continued to work. On Sunday he felt better, went into a saloon, drank two glasses of beer, and started to play cards, when he suddenly became ill. He went to see his father, but felt so ill indoors that he went outside for fresh air; immediately on coming into the air, however, he fell to the ground unconscious and was

carried back into the house. A doctor who was called gave the following report of the symptoms: skin blue-gray; pupils dilated; respiration retarded; pulse weak and irregular; patient unconscious. The man regained consciousness on the following day, and complained of pains in his head, his stomach, and his back. On July 30, 1906, the patient was found to have a chronic gastritis; his hemoglobin was 125 per cent and his red-cell count was 6,500,000. His intelligence and sense of perception had become dimmed. By July, 1908, his muscles had become atrophied, and he was extremely emaciated. His blood examination showed the following: red-cell count, 5,600,000; hemoglobin, 80 per cent; lymphocytes, 32 per cent; polymorphonuclear leucocytes, 47 per cent; eosinophiles, 20 per cent. By October, 1909, his memory had failed; otherwise he was in about the same condition as in 1908. In 1911 he was asked the date; he looked for a calendar and said that he did not know whether it was 1910 or 1911. His perception of distances had failed also. On October 4, 1912, he was visited by the doctor. When asked whether he recognized the doctor, he said that he had seen him before, but where and when he could not recall; thus he showed loss of perception of both time and space. He gave correctly the names of his children but could not remember which was the eldest. In March, 1913, his condition was about the same. If he wandered some distance from his home he was unable to find his way back. Several other incidents revealed the loss of perception of time and space.

Grafe and Homberger believe that the type of psychosis shown by this patient is identical with Korsakoff's syndrome, in which there is a loss of memory not only of things occurring before the accident but also of things occurring afterward. However, a careful analysis of the symptoms as recorded brings out the probability that the loss of perception of time and space was the principal feature; and this, according to Jelliffe (1913), indicates cerebellar lesions.

Taylor (quoted by Adams, 1912) reports the case of a young man who worked in a chemical laboratory. The report states that the young man placed one or two drops of nitrobenzene on his tongue in order to remove the odor of a pipe he had been smoking. He repeated this action one and one-half hours later. In a few hours he was seized with convulsions and became unconscious. The coma lasted for about six hours, but the patient died in about fifteen hours after regaining consciousness.

Another case of fatal poisoning resulting from a small amount of nitrobenzene is reported by Stone (1904). The report states that a strong man, weighing one hundred and sixty pounds, had stained the uppers of a pair of shoes with liquid shoe-blacking. He put the shoes on before they were dry and spent the evening in a café. About midnight he fell to the floor unconscious, and he died a few hours later.

These two cases are interesting from the fact that small quantities of the drug were able to produce death. Absorption in each case was probably facilitated by the presence in the blood of some solvent for nitrobenzene. In the latter case, the ingestion of alcoholic liquor undoubtedly facilitated the absorption thru the skin.

On the other hand, a number of cases have been reported in which the patient recovered after the ingestion of large quantities of nitrobenzene. Two interesting examples are as follows:

Dodd (1891) reports the case of a man forty-seven years of age, who ingested two drams of nitrobenzene. The resulting symptoms were vomiting, extreme cyanosis, fixed jaws, contracted pupils. The patient eventually recovered.

Schild (quoted by Adams, 1912) reports the cases of three girls who took nitrobenzene as an abortifacient. The approximate amounts taken were as follows: one ingested 5 mils, and recovered; the second ingested 16 mils, and recovered; the third took 16 mils, and died.

### CLINICAL SYMPTOMS OF POISONING

Regarding the characteristic clinical symptoms of nitrobenzene poisoning, Türk (quoted by Roth, 1913) says:[6] "The clinical picture consists on the one hand of a greater or less stimulation of the gastro-intestinal tract; secondly, of changes in the blood which consist of the formation of methemoglobin and destruction of erythrocytes, with associated phenomena of high-grade cyanosis, blue skin color, later icterus, dyspnoea, etc." Weisstein (1892) says that there is great variation in the symptoms. He says that those symptoms which might be called characteristic are:

> Great dyspnoea, livid, cyanotic color of the skin, and characteristic bitter-almond-oil odor of the breath; even the urine may have this odor. In addition we may have symptoms which are not exactly characteristic, as they are inconstant, such as incoordination, hesitating speech, drowsiness, numbness, vomiting, convulsions, coma, dilation or contraction of pupils, or unequal dilation, nystagmus, irregular pulse. Death is due to a failure of respiration and circulation. In animals and in man the symptoms may appear early or late, even days late.[6]

[6] Translation from the original German.

Weisstein states further that the lethal dose depends on the form in which the dose is taken, the condition of the stomach at the time of taking, and other factors.

### SEAT OF ACTION OF THE DRUG

Regarding the specific tissues acted upon by nitrobenzene, there has been much speculation. Roth (1913) writes as follows:[7] "The action of nitrobenzene depends, as is known, upon blood changes. Hence hematological changes have excited the greatest interest, tho in different cases the findings differ greatly." Some writers report pronounced hemolysis accompanied by leucocytosis, and those who have subjected the blood of patients poisoned by nitrobenzene to spectroscopic analysis have for the most part found an absorption band occupying nearly the same position as the methemoglobin band. Some have regarded this band as the methemoglobin band and have concluded that methemoglobin is formed in the blood in cases of nitrobenzene poisoning. Others claim that the band is distinct from the methemoglobin band and is peculiar to nitrobenzene alone. A discussion of these findings appears on a later page of this article. The following notes on the observations of blood changes in clinical cases may be of interest:

Roth (1913) reports the case of a woman who drank nitrobenzene to produce abortion. Her blood became dark chocolate in color. The red-cell count dropped from 4,662,000 to 3,840,000; the hemoglobin dropped from 98 to 80 per cent; the number of leucocytes dropped from 16,840 to 9400; and the lymphocytes rose from 14.4 to 22.3 per cent. There was no methemoglobin in the centrifugalized blood serum, but methemoglobin appeared in the red corpuscles. Hence Roth concludes that methemoglobin is formed inside the red corpuscles. He thinks that the formation of methemoglobin is due to the action of p-aminophenol, formed from the nitrobenzene.

Meyer (1905) reports the case of a patient who took about a teaspoonful of nitrobenzene, presumably to produce abortion, on June 15. On the 16th and 17th of the month the body temperature was 38° C. The red-cell count dropped to 2,180,000; the white-cell count dropped to 5200; the hemoglobin was 54 per cent. There was no morphological change in the red corpuscles.

[7] Translation from the original German.

Massini (1910–11) cites two cases. The first is that of a man thirty years old, a worker in a chemical laboratory, who on November 30 drank by mistake 30 mils of nitrobenzene. Vomiting was at once induced by giving $1\frac{1}{2}$ grams of copper sulfate in 50 mils of water. The color of the blood was dark brown until December 3. The red-cell count had dropped to 1,800,000 by December 9, but returned to normal by January 11. The white-cell count was 22,400 on December 7, and 6800 on January 11. The lymphocytes rose from 22.5 per cent on December 2 to 41.7 per cent on December 26. The polymorphonuclears dropped from 76.8 per cent on December 11 to 54.7 per cent on December 26.

The second case cited by Massini is one of chronic poisoning in a man thirty years old, who worked in a room with nitrobenzene. He was poorly nourished, the color of his skin was blue-gray, the spleen was enlarged, the urine was very dark, and urobilin was detected by spectroscopic analysis. The man was admitted to the hospital on June 4. The red-cell count was then 2,500,000, but it had risen to 4,300,000 by June 29. The white-cell count was 6000 on June 4, had risen to 8400 by June 8, and had dropped to 3800 by June 24. A microscopic examination of the blood revealed embryonal forms.

Bondi (1894) reports the case of a man twenty-five years old, who drank a "mandel liqueur" at nine o'clock in the evening. He was admitted to the hospital at four o'clock in the afternoon of the following day. The red-cell count was 6,340,000, the white-cell count 16,000; there was no methemoglobin; the hemoglobin was 112 per cent. Only one examination was made.

### EXPERIMENTAL CASES OF POISONING

The literature dealing with experiments on animals is not very considerable. Only twice have intensive experiments been carried on, by Letheby (1865) and by Filehne (1878). It may therefore be well to include here a short abstract of the literature dealing with the subject from the experimental side.

The first experiment recorded was conducted by Jones (1857). He gave one dram of nitrobenzene to a rabbit, and reports that the rabbit was killed instantly. One-half dram of nitrobenzene in two drams of water, given internally, killed a cat within twelve hours. This writer gives no reference to earlier works, nor does he describe the symptoms

of nitrobenzene poisoning. He had been working on the toxic properties of a commercial oil of bitter almonds which was known to contain hydrocyanic acid. The experiments with nitrobenzene were conducted as a side issue and the purity of the nitrobenzene is doubtful.

Casper (1859) was led to experiment with nitrobenzene because in post-mortem examinations of cases of poisoning, the cause of which had been diagnosed as hydrocyanic acid, he often detected the odor of nitrobenzene in the tissues. He mentioned the desirability of learning whether this drug was poisonous, since it was being used more or less extensively in the perfuming of soaps, pomades, and the like, and stated that so far as he knew there was no account of it as a poison. His article contains a short account of the chemical and physical properties of the drug. In his experimental work he gave an ounce of nitrobenzene (purity not stated) to a rabbit in four separate doses at intervals of fifteen minutes. Within a few minutes after the final dose, the animal fell suddenly on its left side. Its pupils were dilated. Convulsions occurred which involved the entire body, and within a few minutes the animal was dead. The body was allowed to remain untouched for a period of twenty-four hours in order to simulate forensic post-mortem cases. It was then opened. No odor of nitrobenzene was detected either externally or in the lower part of the digestive tract, but when the skull was opened a strong odor of nitrobenzene was given off. This odor was so pronounced that a newcomer, who was wholly unaware of the experiment, at once spoke of "almond oil." The odor was detected in the blood, in the brain, and in other tissues. The body was placed in a cellar for two weeks and at the end of that time had lost but very little of the odor.

F. Hoppe (reported by Casper, 1859) introduced 20 mils of nitrobenzene into the stomach of a medium-sized dog. After a few hours the dog appeared stupid, and at the end of twelve hours it was found in a deep coma. Respiration was slow and the skin temperature was lowered. The animal was killed by pithing without causing convulsions. Blood drawn from the subclavian vein was dark brown in color, and the odor of nitrobenzene was detected in it. The same odor was detected in the urine, which was dark brown, in the bile, and in all the organs. The stomach contained a few drops of nitrobenzene, and the contents of the stomach were strongly alkaline. The blood retained the odor of the drug for several days. Casper concludes that these experi-

ments prove nitrobenzene to be a poison; and that a distinction between cases of poisoning by nitrobenzene and by hydrocyanic acid can be readily made, since the bitter-almond-oil odor due to hydrocyanic acid disappears within three or four days — the chemical (hydrocyanic acid) being destroyed by contact with the tissues — while the same odor due to nitrobenzene will persist for several days.

Ollivier and Bergeron (1863) were led to study the action of nitrobenzene from the same standpoint as was Casper — that is, because the drug was being extensively used in perfuming toilet soaps and in making flavoring extracts. It had also been recommended and used with friction for the cure of parasitic affections. These investigators argued that since nitrobenzene is readily converted into anilin thru the action of nascent hydrogen, it is conceivable that it may be changed into anilin in the human body, and anilin is a poison. They gave a guinea pig ten or twelve drops of nitrobenzene. The animal, after the initial agitation and profuse salivation, remained motionless for some time and then began to run about again without showing the least signs of ill effects from the drug. To another guinea pig they gave approximately three grams. The experiment was begun at 2.12 o'clock, and at 2.40 the animal exhibited tremors without excessive convulsions. The heart beats were very faint and the respiration was decidedly labored. At 3.10 the animal attempted to turn around and fell on its right side. The animal died a few minutes before 4 o'clock.

In another experiment Ollivier and Bergeron exposed the muscles of a frog's leg and placed on them a drop of nitrobenzene. The muscles remained sensitive to electric stimulations for a long time and did not show the slightest histological changes. The investigators then exposed the heart of a living frog and placed a few drops of nitrobenzene on it without obtaining the slightest modifications of the heart beat.

In a fifth experiment Ollivier and Bergeron gave a large, healthy dog six drams of nitrobenzene, and in a half hour an additional dose of five drams. The experiment was begun at 12.40 o'clock. The animal appeared agitated and secreted saliva profusely, but did not vomit. Finally it lay down in a dark corner and remained motionless for some time. At 1.20 it started to howl, appeared excited, and moved its head convulsively. Its tongue was hanging out and its eyes were wide and animated. This condition lasted for about six minutes, when the dog again became motion-

less. At 5 o'clock it showed tremors, and about an hour later its hind extremities were paralyzed. On the following morning it was found dead and rigid. A post-mortem examination showed the following: The blood was about normal, the cells being little altered, but the blood plasma contained fine, oily droplets which were recognized to be nitrobenzene. The meninges were congested, the veins turgid, the tongue and mucosae violet in color, and there was a stasis of the blood in the capillaries. The heart was dilated and filled with viscous blood, but there were no clots. The authors claim to have found anilin in some of the organs and in the blood, as well as nitrobenzene. They state that they had tested the nitrobenzene for the presence of anilin just prior to the experiments and had not found a single trace. Hence they conclude that their original assumption was correct — that nitrobenzene may be converted into anilin in the living body of an animal.

In another experiment these investigators caused a young dog to ingest a daily dose of from two to three grams of the drug for a period of sixteen days. They then killed the dog. They found no trace of anilin in any of the organs except the spleen and the liver.

From these experiments Ollivier and Bergeron draw the following conclusions: (1) that death due to nitrobenzene poisoning is delayed as compared with death due to an equal dose of anilin; (2) that nitrobenzene given in small daily doses is eliminated in part as such, and changed in part to anilin, which accumulates in the spleen and liver; (3) that the drug is in time eliminated as nitrobenzene and anilin, and is not changed into picric acid; (4) that animals poisoned by nitrobenzene die with symptoms of asphyxiation; (5) that the symptoms preceding death are similar to those in the case of anilin poisoning, except that the animal exhibits tremors, not convulsions of the whole body as in the case of anilin poisoning; (6) that nitrobenzene does not appear to cause any direct alteration of the blood, the muscles, the heart, the nerves, or other organs.[8]

In a further experiment with nitrobenzene, these authors placed guinea pigs, cats, and other small animals under a bell jar and introduced air saturated with the vapor of nitrobenzene, allowing a small opening for ventilation. Under these conditions they were able to produce death in from two to five hours, death being preceded by characteristic symptoms such as staggering, tremors, and paralysis of the hind legs.

[8] The staining of nerve cells by the Nissl method was not developed until 1885.

Letheby (1865) carried out a number of experiments for the purpose of studying the effects of nitrobenzene on dogs and cats. The drug was invariably administered by introducing it into the stomach. The results obtained in his various experiments were fairly similar; therefore the following report (page 49 of reference cited), which is quoted verbatim, may be taken as characteristic of the results obtained by him:

Experiment 2.— January 16th, 1862, at half-past three p. m., I gave half a drachm of nitro-benzole to a small terrier dog. The poison was poured into the animal's mouth; it caused discomfort, as if from the unpleasant taste, and produced a copious flow of frothy saliva. This, however, soon subsided, and for an hour there was no perceptible effect beyond a little heaviness of look. At the end of an hour the animal was sick, and after that it became sleepy. In another hour it was again sick, and again in a quarter of an hour. For four hours the animal lay on its side asleep, and then some water was given to it, which it took freely; from that time till midnight nothing appeared to be the matter with it, and the next morning it seemed to be quite well, and ate its food heartily. It remained thus all day, and was left at night apparently well, but the next morning at half-past six o'clock it was found upon its side insensible. The legs were in constant motion, as if the animal was running. The head was drawn back, and the muscles of the neck were rigid, as if in spasm; the eyes were open, the pupils were widely dilated, and the conjunctiva was insensible to the touch. The animal lay in this state for sixty-six hours, that is, nearly three days, and then it died as if from exhaustion. During the whole of this time the legs were in constant motion; there were occasional spasms, and then a sort of struggle for breath. The heart beat in an irregular, tumultuous manner, and the breathing was somewhat laborious. The total time which elapsed from the taking of the poison to the death was one hundred and four and a half hours.

The body was opened twelve hours after death. The brain and its membranes were very vascular; there was no odour of the poison in any part of the body; the lungs were slightly congested; the heart was full of blood on the right side, and there was a little on the left; the liver was of a deep purple colour; the gall-bladder was full of bile; the stomach was nearly empty, it only contained a little fluid and mucus; there was no sign of irritation. On analysis it yielded a trace of aniline, but no nitro-benzole; and nothing was found in the brain.

Letheby divided the action of nitrobenzene into two classes, characterized respectively by rapidly developing coma and by slow paralysis and coma after a considerable period of inaction. He summarizes the symptoms as follows (page 42 of reference):

When the effects were speedily fatal, the animals were soon seized with giddiness and an inability to walk. The weakness of the limbs first appeared in the hind extremities, and was manifested by a difficulty in standing; but very soon it extended to the fore legs, and then to the head and neck. There was complete loss of voluntary power; the animals lay upon the side with the head drawn a little back, and with the limbs in constant motion, as if in the act of trotting or running. The muscles of the back were occasionally fixed in spasm, and every now and then the animals had a sort of epileptic fit. They looked distressed, and howled as if in pain, and struggled violently; after which they always seemed exhausted, and lay powerless. The pupils were widely dilated, the action of the heart was tumultuous and irregular, and the breathing was somewhat difficult. For some time, however, the animals retained their consciousness, and gave signs of intelligence when spoken to; but suddenly, and often at the close of a fit, they became comatose, the eyes remaining open, although the conjunctiva was insensible to touch, and the movements of the limbs would nearly cease, the breathing became slow and somewhat stertorous, and the animals seemed to be in a

deep sleep. This condition generally lasted until they died — the duration of the effects being from twenty-five minutes to twelve hours after the administration of the poison.

When the action of the poison was slower there was often no visible effect for hours or days. At first there was always a little discomfort from the taste of the oil; but this soon subsided, and then the animals appeared to be in perfect health for a day or more; they would run about as lively as usual, and would eat their food heartily; but suddenly there would be a look of distress, and perhaps an attack of vomiting, and then a fit of epilepsy. When this had subsided the animals were weak, and sometimes they were paralyzed in the hind extremities. After two or three of such attacks, the loss of power extended to the fore limbs, and then they would lie upon the side in a perfectly helpless condition; after which the progress of the case was much the same as that already described, except that it was considerably slower: consciousness, for example, would be retained for days after the paralysis had set in; and although the animals were quite unable to stand, they would take food and drink when they were put into the mouth; in fact the condition in which they lay was most distressing; the look was anxious and full of fear, the limbs were in constant motion, and every now and then there would be a violent struggle, as if the creature was in a fit, or was making fruitless efforts to rise. This would last for days, and then there would be either a gradual restoration of voluntary power, with complete recovery, or death from exhaustion. The time which elapsed from the administration of the poison to the coming on of the first serious symptom — the epileptic fit — varied from nineteen hours to seventy-two: in most cases it was about two days, and the time of death was from four to nine days.

Letheby explains the long period of inaction as being due to the time required for the conversion of nitrobenzene into anilin. He does not explain the reason for the difference between the two types of effects. Guttmann (1866) thinks this is not the real explanation of the latent period, for if an animal were given only from thirty to sixty drops of nitrobenzene there would not be enough in the body to form anilin since nitrobenzene is continuously excreted by the lungs. Guttmann states, furthermore, that according to Bergmann two grams of anilin is not fatal to a small dog, and therefore from thirty to sixty drops of nitrobenzene could not be fatal if it were all converted into anilin.

Guttmann carried out experiments on frogs, rabbits, pigeons, and chickens. He states that in frogs he obtained paralysis of all movements and the abolition of all reflexes. This result was obtained whether the drug was given by mouth, by injection under the skin, or by exposure of the frog to the vapor under a bell jar. He concludes that since the muscles reacted to stimuli, the action of the drug was central, in contrast with that of curare and coniin, which act on the peripheral nerve structures. His paralyzed frogs did not recover. Dresbach (Dresbach and Chandler, 1917) obtained only depressant action on frogs, but in his experiments frogs that were paralyzed for from one and one-half to two hours recovered. Guttmann produced death in rabbits by placing in the mouth as little as $\frac{1}{2}$ mil of the drug. The symptoms reported were unsteadiness, staggering, loss of reflexes, wide pupils. Death resulted in each case in about

twelve hours. Post-mortem examinations showed dark blood, congestion of the brain membranes, and a pronounced odor of nitrobenzene in the tissues. All the organs were normal. (It will be remembered that Ollivier and Bergeron were unable to detect the odor of the drug in the tissues of a poisoned animal.) After introducing 1 mil of nitrobenzene into the mouth of a hen, Guttmann observed that the bird closed its eyes and had an unsteady gait, but recovered shortly. Later he gave 2 mils to the same bird, and it quickly became unconscious and died during the night. The brain was hyperemic, as in the case of the rabbits.

In regard to the action of the vapor, Guttmann states that Charvet breathed a " thick vapor " of nitrobenzene for several hours without ill effects, altho he had seen complete anesthesia and sleep produced in a dog after an exposure of one and a half hours to the vapor. He also says that Buisson denies that the vapor has any narcotic effect, and moreover that Ollivier and Bergeron killed cats and guinea pigs by exposing them to the vapor for from two to three hours. Guttman therefore placed pigeons under a bell jar and caused them to breathe the vapor of the drug. He observed no effects after an exposure of one hour, but produced death by an exposure of from two to three hours. He states that the symptoms are the same after vapor inhalation as after subcutaneous injections or after ingestion of the liquid. Guttmann did not observe convulsions in the animals poisoned, nor did he have a very long latent period as described by Letheby. He could not explain the latent period, but believed that Letheby's explanation was not correct, since in rabbits killed by ingesting four grams of nitrobenzene he could find no trace of anilin in the urine or in the organs. He used the calcium-hypochlorite test. He observes that Bergmann, who also could find no anilin in the tissues of the poisoned animals, ascribes the cause of the latent period to slow absorption of the drug; but Guttmann points out that this theory is not in accord with the cause of the rapid action which is often produced. He also found nitrobenzene in the blood of rabbits twenty-five minutes after subcutaneous injections.

Eulenberg (1876) killed a cat by exposing it to the vapor of nitrobenzene under a bell jar. He describes the symptoms as staggering, stupor, and so on. He states that the action of the vapor is more rapid than the action of the liquid. This contradicts Guttmann, who found the action of the vapor slower. Eulenberg could find no trace of anilin.

Filehne (1878) undertook experiments for the purpose of clearing up some of the questions concerning which the findings of other writers varied in their essential details. Those questions were: What is the reason for the latent period? Is nitrobenzene converted into hydrocyanic acid in the body? Is it converted into anilin in the body? What is the action of nitrobenzene on respiration and on the blood? Filehne also includes among his list of problems the following: spectroscopic analysis of the blood of animals poisoned experimentally by nitrobenzene; the action of nitrobenzene on blood outside of the animal; the action of nitrobenzene on the nervous system and on muscle tissue; and the therapeutic principles to be employed in treating cases of nitrobenzene poisoning.

Filehne maintains that the explanation of the latent period on the basis of time required for the absorption of the drug is not sufficient, since it cannot explain the extremely rapid course of the drug in some cases. Furthermore, Filehne found nitrobenzene in the blood within twenty-five minutes after it had been injected subcutaneously; he states also that animals heavily poisoned very quickly exhale nitrobenzene in sufficient amounts to perfume large volumes of water. He further claims that the latent period does not depend on an accumulative action of the drug, since a single drop introduced directly into the blood stream of a rabbit will kill the animal instantly. He thinks that the rapidity of the action depends on the rate in which the nitrobenzene passes from the blood to the central nervous system. In cases exhibiting rapid action the transfer takes place quickly and convulsions result (in dogs), while if the transfer takes place slowly the action is retarded and paralysis is the principal symptom. In the frog, Filehne observed only paralysis. He was able to produce rigor mortis also in the hind leg of a frog immediately after injecting nitrobenzene into the aorta, even in cases when the muscles had been severed from their connection with the central nervous system by cutting the ischiadic plexus, thus showing that nitrobenzene does exert a direct action on the muscle tissue. Filehne argues that the reason why Ollivier and Bergeron failed to show any action of the drug on the exposed frog leg was that the lymph in which the muscles are bathed may have served to exclude the drug from direct contact with the muscles. He writes that he himself has observed similar results when the muscles were thus protected.

Filehne claims that nitrobenzene is not converted into hydrocyanic acid in the body, since, in the first place, the blood of animals poisoned by hydrocyanic acid is red while that of animals poisoned by nitrobenzene is dark brown; then, too, the action of hydrocyanic acid on muscle tissue is different from that of nitrobenzene, as Filehne was able to prove by experiments on frogs; furthermore, Filehne was unable to detect the slightest trace of hydrocyanic acid in the blood or other tissues of animals poisoned by nitrobenzene, even by tests so delicate as to detect the drug in dilutions of 0.0002 per cent.

Nor will Filehne concede that nitrobenzene is converted into anilin in the body. He was unable to find any trace of it, as were also Bergmann and Guttmann. He shows that Letheby's method was at fault; that, according to Hoffmann and Muspratt, nitrobenzene when heated with alcoholic potash is converted into azobenzol, oxalic acid, and anilin. (Letheby apparently used the phenylisocyanide test, whereas Filehne applied the hypochlorite test.)

Regarding the action of nitrobenzene on the blood, Filehne found that in frogs and mammals the blood was dark brown after poisoning by nitrobenzene, except in the case of rabbits, which, he thinks, die before the drug can act on the blood. He could find no morphological changes in the blood-cells, but by spectroscopic analysis he found an absorption band occupying a position between C and D near the position occupied by the absorption band of acid hematin. He called this band the *nitrobenzol band*. It is possible that he was not familiar with the methemoglobin band, since the formation of methemoglobin was demonstrated only a few years prior to his experiments. Filehne was unable to produce the dark brown color in arterial blood by shaking it directly with nitrobenzene; he makes no statement regarding venous blood. By blood-gas analysis he demonstrated that the blood of animals poisoned by nitrobenzene had lost its ability to take up oxygen. He found the oxygen content of such blood to be less than 1 per cent, as against the normal 17 per cent, while the carbon dioxide content had increased in both absolute and relative amount.

Filehne states that the toxicologists have placed the convulsion-producing poisons in two categories: (1) those that produce convulsions in both frogs and warm-blooded animals (specific convulsion-producing poisons); and (2) those that do not produce convulsions in frogs but do produce convulsions

in warm-blooded animals, which convulsions are of a secondary nature (as in the case of asphyxia of the brain tissues) and not due to a direct action of the drug on the nervous system. He believes that nitrobenzene does not belong to either of these categories, since all the symptoms — nystagmus, pupil reactions, and the duration of the convulsions — point to a direct action of the drug on the central motor apparatus and yet the drug does not produce convulsions in frogs. He says (page 372 of reference cited),

dass die bei Nitrobenzolvergiftung auftretenden Krämpfe nicht secundärer Natur sind, dass vielmehr das Nitrobenzol direct erregend auf motorische Centralapparate der Warmblüterwirke. Und zwar ist diese Erregung um so heftiger je schneller der Uebertritt des Nitrobenzols aus dem Blute in das Protoplasma der Ganglienzelle erfolgt.

He places nitrobenzene in the list with alcohol, ether, and the like, which exert a direct action on the central nervous system.

Regarding therapeutics in cases of nitrobenzene poisoning, Filehne says that solvents for this drug, such as alcohols, milk, and oils, are to be avoided. He recommends blood transfusions. He believes that the use of nitrobenzene for flavoring foods, in flavoring extracts, and in alcoholic drinks such as liqueurs, should be prohibited.

One other monograph may be mentioned, a paper by Zieger (1903). Zieger followed a method similar to the one used in the present research, but his technique was faulty in several respects and he used only a small number of animals — cats and rabbits. He says that nitrobenzol acts on the brain and respiratory organs and on the blood. He concludes that the vapor is not especially toxic when inhaled in amounts ordinarily met with, but that absorption of nitrobenzol from the skin can take place readily with serious results.

## RÉSUMÉ OF THE LITERATURE

From the literature here reviewed it will be seen that the following points appear to be fairly well established:

1. That nitrobenzene exhibits toxic properties, whether it is ingested, applied to the skin, inhaled, or administered by subcutaneous injection.
2. That the size of the lethal dose is extremely variable.
3. That the symptoms of poisoning are inconstant.
4. That an interval of time (the latent period) often elapses between the administration of the poison and the onset of the symptoms.

5. That nitrobenzene is not necessarily converted in the body into anilin, hydrocyanic acid, or any other substance before it exerts a toxic action.

6. That nitrobenzene forms methemoglobin in the blood.

The following points, altho suggested, have not been satisfactorily explained:

1. The exact seat of action of nitrobenzene.
2. The cause of the latent period.
3. The reasons for the variability of the size of the lethal dose.
4. The reasons for the inconstancy of the symptoms of poisoning.
5. The significance of the various types of symptoms observed.

## APPARATUS AND TECHNIQUE OF PRESENT EXPERIMENTS

### APPARATUS

The apparatus used in these experiments was designed after a considerable period of experimentation with various devices; and, since it is such as may be used for investigating the physiological actions of a great many different gases, the principal parts are here described more or less in detail.

The apparatus consists primarily of a fumigation chamber, with accessory devices for saturating, dehydrating, and aerating this chamber. In addition apparatus was provided for determining the purity of the nitrobenzene used, such as devices for ascertaining the boiling point, the freezing point, and so on; and apparatus for determining approximately the amount of nitrobenzene vapor to a cubic foot of space within the fumigation chamber.

The fumigation chamber consists of a galvanized iron tank 60 inches long, 40 inches wide, and 30 inches deep. These dimensions were chosen so that the tank could be readily carried thru doorways. The chamber has a capacity of 43.75 cubic feet. A metal fossa, $\frac{1}{2}$ inch wide and $\frac{3}{4}$ inch deep, was constructed around the outer top edge, to receive the rim of the cover. When it was desirable to seal the tank, the cover was placed on and melted paraffin was poured into the fossa, thus rendering the tank air-tight. The cover is provided with two glass windows, one 8 x 10 inches and the other 12 x 18 inches. The larger window is removable, and fits into a slot in such a way that it can be sealed and unsealed readily;

paraffin is used for effecting an air-tight seal. It was thru this opening that animals were introduced into the tank, thus obviating the necessity of removing the entire cover each time. A small glass window was also built into one side of the tank, thru which observations of the temperature inside could be made. The tank rests on two runners, one of which is lower than the other in order to provide a slant to facilitate drainage of urine thru a small hole in one corner of the bottom of the tank. A false removable bottom 1 inch in height, made of strong wire of No. 2 mesh and well supported, was constructed in three pieces, for ease in handling. This false bottom serves to keep the animal from contact with its excretions. Two parallel steel supports are placed across the width of the tank $1\frac{1}{2}$ feet above the bottom, and on the middle of these supports rests a wire cage 8 x 8 x 10 inches. This cage serves to protect a small fan, which is connected to a motor on the outside by a shaft passing thru a tightly fitting collar in one side of the tank. This cage also protected a triangular strip of cheesecloth from which the nitrobenzene was evaporated. The container into which the cheesecloth dipped rested on an aluminum tray in the bottom of the cage. The inside of the tank and all its internal accessories were coated with paraffin in order to prevent rusting.

## TECHNIQUE

### *Obtaining pure nitrobenzene*

Practically pure nitrobenzene was obtained by redistilling the commercial liquid, at the temperature of the boiling point of nitrobenzene, until a product was obtained which proved experimentally to have a boiling point and a freezing point corresponding to pure nitrobenzene (page 412).

### *Aeration of the fumigation chamber*

The tank was aerated by passing air saturated with nitrobenzene into it at a rate determined by the weight of the animal being fumigated. The air was saturated by passing it, after dehydration, thru a flask containing nitrobenzene and kept at a temperature of 50° C., and condensing it by passing it thru a series of U-tubes containing nitrobenzene. The final condensing tubes were placed inside the tank, so that the final condensing temperature equaled the temperature of the tank.

That this method for saturating air with nitrobenzene is practical was shown experimentally in the following way: A glass-stoppered U-tube containing a little nitrobenzene was dehydrated and weighed to constant weight. This U-tube was then placed in a constant temperature chamber, which was also a desiccator, with the final condensing tube, and air from this condensing tube was passed thru the U-tube for a given period of time. The U-tube was then reweighed, and the fact that it had neither lost nor gained in weight indicated that the air coming from the final condenser was saturated.

### *Maintaining constant temperature*

A constant temperature $\pm 1$ degree centigrade was maintained in the fumigation chamber by regulating the temperature of the room, it being found that a direct relation existed between these two temperatures.

### *Histological technique*

In preparing sections for histological studies the following technique was employed.

The animal was quickly and painlessly killed by piercing the heart with a scalpel, since it was important that death should be produced without the use of drugs and in a manner which would produce a minimum shock. The body was opened immediately, a cannula was connected with the aorta, and a warm (normal body temperature) isotonic saline solution was transfused until all the blood was washed out. The saline solution was immediately followed by the warm fixing fluid, which consisted of 4-per-cent formaldehyde in a saturated aqueous solution of corrosive sublimate. The brain and the cord were then quickly dissected out, small pieces from each being placed directly in the fixing fluid and allowed to remain for twenty-four hours. The pieces were then washed in running water for twenty-four hours, after which they were carried thru 50-, 60-, 70-, and 82-per-cent alcohol. They were allowed to remain in 82-per-cent alcohol, to which was added a few drops of 5-per-cent alcoholic iodine, until the excess corrosive sublimate had been removed. The alcohol was changed twice a day for a time, and then as frequently as it became decolorized. The tissues were then dehydrated, cleared, embedded, and sectioned. The sections were cut 4 and 5 microns thick

and were fixed on slides by the usual methods. They were then cleared and carried down thru the various grades of alcohol to water, and then stained for ten minutes in hot (70° C.) 10-per-cent methylene blue in saturated anilin oil water (Rasmussen and Myers, 1916). When taken from the staining fluid they were hurriedly rinsed in a large volume of water, and were then placed directly in 95-per-cent alcohol where they were allowed to remain until they were sufficiently destained. They were then dehydrated, cleared in xylene, and mounted in balsam. Corresponding tissues from each of the poisoned animals and from the controls were carried thru the same fluids and stained on the same slides.

## DESCRIPTIONS OF EXPERIMENTS

A large number of experiments were carried out. Since, however, the symptoms for each group of animals were in general fairly similar, so far as localizing the action is concerned, only two or three experiments from each group in which the animals showed typical symptoms are included in the descriptions. The other experiments included are those in which the symptoms were different in essential details.

### DOG I (MALE DACHSHUND)

Weight of dog, 16.4 kilograms.

*August 30, 1916* — Dog fumigated at 26° C. for a period of five and one-half hours.[9]

Time when fumigation was begun, 11.15 a. m.
Time when fumigation was finished, 4.45 p. m.

Observations: After having become accustomed to the strangeness of the fumigation chamber, the animal lay down and became quiet. At 2 p. m. it was observed that the dog had vomited, urinated, and defecated. At 3 p. m. the animal was seen to stagger when attempting to walk from one end of the tank to the other. At 4 p. m. the animal was found lying on its side; it was unable to lift its head; its respiration was labored. At 4.30 the condition was about the same. At 4.45 the animal was removed from the tank. The respiration was slow and regular, except for intermittent long, deep inhalations; the animal was unconscious;

[9] The chamber was thoroly dehydrated before the experiment was begun, but in this instance no time was allowed for saturation. Ordinarily sufficient time was given to insure saturation of the chamber before the animal was introduced.

the spinal reflexes were apparently gone; the conjunctival reflexes were present; there was profuse salivation. The muscles of the entire body were wholly relaxed when the animal was removed from the tank, but soon all of the legs became extended and rigid. This condition gradually passed off and the animal showed signs of recovery. By 11.30 p. m. the dog had regained consciousness and was able to stand on its feet. It walked slowly, with a trembling, staggering, uncertain gait and without aim.

*August 31* — The animal was found to have greatly improved. It refused food, however, and howled when the back of its head was touched. It would press its head against the attendant's legs or other objects, and remain thus for hours.

*September 1* — The dog was found normally active, eating meat and drinking water freely. No other effects followed.

*September 22, 1916* — Dog fumigated a second time, this time at 23° C. for a period of six hours.
Time when fumigation was begun, 11.10 a. m.
Time when fumigation was finished, 5.10 p. m.

Observations: At 11.15 a. m. the dog was observed licking its chops. At 11.30 it was panting at intervals as if short of breath. At 12 m. it was slightly drowsy. At 12.05 p. m. it was unsteady, sitting on its haunches but keeping this position apparently with difficulty. At 12.10 it lay down in a natural position and closed its eyes; it would open its eyes when one rapped at the tank, but would immediately close them again. At 12.20 the dog's head was raised and the breathing was slow and labored. At 12.30 the animal appeared slightly confused, and uncertain as to the direction of the sound when one tapped on the tank. At 12.50 the animal stood up when called and walked across the chamber, but immediately went back and lay down again. From that time until 5.10, when it was removed from the tank, the animal lay quiet but alert as if sensing some danger. After the dog was removed from the fumigation chamber fresh vomit was found in the tank, which had probably been emitted while the chamber was being opened. A copious secretion of saliva was observed and the animal was slightly unsteady on its feet. It refused water.

*September 26* — The animal had apparently recovered and no symptoms of the action of the drug appeared until on this day (four days after exposure to the vapor) when the attendant observed that the dog had difficulty in using its hind legs. An examination was made and the animal appeared normal. This was about 9 a. m. By 11 a. m., however, incoordination of the muscles of the hind legs was observed and the animal walked with a peculiar sprawling gait. This condition became more pronounced as the day advanced, and by 3 p. m. it was almost impossible to induce the animal to walk at all. Its tendency was to crawl into dark corners and hide. Finally the animal refused to remain on its feet, and when placed on its feet it would stumble and fall down again. However, at 4.30 p. m., after a considerable period of rest, the dog walked into its kennel with a slow, staggering, sprawling gait.

*September 27* — There was evidence that the dog had thrashed about a good deal during the night and it was found lying prone on its side in the kennel. The animal appeared conscious, but was very irritable and thrashed about considerably. At 3 p. m. pronounced nystagmus was observed; the left pupil was dilated, the right pupil was contracted, and the jaws were set. At 4 p. m. the animal showed a tendency to remain on its left side; when turned on its right side, it executed a right-to-left rotation, finally coming to rest on the left side. The animal seemed to be conscious and wagged its tail when spoken to. The flexor muscles of the hind legs were in a state of tense tonic contraction, drawing the legs up against the body. The animal would neither eat nor drink. The anal temperature was 37.8° C.

*September 28* — The general condition of the animal was about the same. The trunk muscles were tremulous, the extensor leg muscles contracted. The legs were withdrawn once or twice when touched, but finally they failed to react even to the prick of a pin, so tense was the muscular contraction. The animal made swallowing movements and could work its jaws to some extent, swallowing water when placed in its mouth. Nystagmus was not so pronounced. The anal temperature was 38.3° C.

*September 29* — The animal appeared to be somewhat improved. Nystagmus was decreasing. The dog swallowed milk when placed in its mouth. The flexor muscles were relaxed. Clonic movements of the

hind legs were observed. The anal temperature was 39° C. The heart rate was increased only when the animal struggled, but was a trifle irregular.

*September 30* — The animal was very much improved. It ate chopped meat and drank milk, and could raise itself a little. Its head waved about in an uncontrollable manner. The anal temperature was 38.5° C.

*October 1* — Still more improvement was observed. The dog could almost regain its feet. It refused water, but drank milk without urging. In the afternoon the animal was able to stand on its feet; it walked eight or ten steps, and then staggered and fell. The anal temperature was 38.7° C.

*October 2* — The animal walked fairly well, but staggered a great deal. It ate greedily.

*October 3* — The animal had regained nearly the normal use of its legs and was found running about with other dogs. This dog finally recovered entirely and never developed any further symptoms.

It is interesting to note that this animal exhibited symptoms just the reverse of those described by Filehne as following a retarded action of the drug (page 424).

DOG II (MALE)

Weight of dog, 11.5 kilograms.

*September 1, 1916* — Dog fumigated at 25° C. for a period of two hours and fifty-nine minutes.
Time when fumigation was begun, 12.40 p. m.
Time when fumigation was finished, 3.39 p. m.

Observations: Soon after being introduced into the chamber, the animal was observed to lick its chops; it panted at intervals; respiration was accelerated. At 1.45 the animal appeared restless, howling a good deal; it appeared to stagger. At 2.30 the animal was unable to remain on its feet; it lay on its side, with the extensors of all legs in tonic convulsions. At 2.50 the condition was about the same as at 2.30. At 3 p. m. the dog made sounds as if it was becoming anesthetized; there were clonic convulsions of the extensor muscles of the fore legs, and occasional clonic convulsions of the extensors of the hind legs followed by general abdominal

muscle tremors; respiration was quickened, with periodic long, deep inhalations; the dog was apparently unconscious, and could not be aroused; the eyes were open and winking; there was nothing abnormal about the pupils, and no nystagmus. At 3.04 the condition was about the same; the dog moaned at intervals. At 3.24 the respiration was 40, and increased in depth with periodic long, deep inhalations as before. At 3.25 there was opisthotonos, the convulsions lasting for about one-half minute and being followed by accelerated respiration. At 3.27 the respiration was 52. At 3.35 the respiration was shallow. At 3.39 the animal was removed from the tank; the muscles of the entire body were relaxed, but soon the leg muscles stiffened; the tongue and the lips were cyanotic. At 3.40 the respiration was irregular, gasping; the animal was given artificial respiration and oxygen, but it died at 3.50.

The body was opened immediately. The heart blood was of a chocolate color; the lungs were a dark gray; the intestines were hyperemic; the liver and the spleen were coffee-colored.

In this case the type of symptoms described by Filehne as following a rapid action of the drug were undoubtedly shown.

### DOG IV (FEMALE)

Weight of dog, about 12 kilograms.

*September 27, 1916* — Dog fumigated at 21.5° C. for a period of ten hours.
Time when fumigation was begun, 8.30 a. m.
Time when fumigation was finished, 6.30 p. m.

Observations: Immediately after being introduced into the fumigation chamber the animal lay down and went to sleep. It scarcely moved from this position during the entire ten hours; when the observer tapped on the tank the animal would open its eyes; when the tapping was loud it raised its head but seemed confused and could not follow the sound. At 4.30 p. m. the respiration was observed to be decidedly increased. At 5 p. m. the observer tapped loudly on the tank, and the animal opened its eyes but did not raise its head, tho it appeared normal. When removed from the tank at 6.30, the animal was lively, eating and drinking freely, and depositing a great quantity of apparently normal urine. This animal developed no symptoms of poisoning afterward.

DOG V (FEMALE)

Weight of dog, 11.2 kilograms.

*October 26, 1916* — Dog fumigated at 20° C. for a period of twelve hours.
Time when fumigation was begun, 8.30 a. m.
Time when fumigation was finished, 8.30 p. m.

Observations: The animal rested quietly during the entire course of the experiment, and was removed from the tank apparently unharmed. It ate heartily of roast beef and showed no symptoms of poisoning during the next three days.

*October 29* — The animal vomited when it was taken out of the kennel, but no other symptoms were especially noted during the day.

*October 30* — The animal was found on its side and was unable to stand. The following symptoms were observed: lack of coordination of the muscles of the extremities; neck muscles rigid and head drawn back on the body; ventroflexion of back; fore legs drawn up to the body; one or both hind legs involved in clonic convulsions; nystagmus.

*October 31* — The condition was slightly improved. The fore legs were drawn up as before; the hind legs were extended, but were flexed on the body. The right pupil was widely dilated and the left pupil was contracted; this is just the reverse of the pupillary reactions observed in Dog I. Nystagmus was still in evidence. The neck muscles were not so rigid. The dog was very restless all day, but quieted down toward evening. It swallowed milk when placed in its mouth.

*November 1* — There were no signs of nystagmus. The general condition was very much improved. The dog swallowed milk when placed in its mouth. The leg muscles were not particularly involved. Both pupils were widely dilated. The animal appeared to be conscious but did not howl.

*November 2* — The dog's condition was very much improved. It noticed the observer as soon as he entered the room. The animal took milk freely. Nystagmus was observed at times. The pupils were somewhat dilated. The animal was able to raise its head.

*November 3* — The condition was still more improved. The animal drank milk and water readily. Its head was raised. Its fore legs were folded beneath the body, but were stiff.

*November 4* — The animal was able to stand but was unsteady on its feet. It ate meat and drank milk and water.

*November 5* — The condition was about normal. The dog's appetite was good. The heart and the respiration were apparently not affected in this case.

*January 20, 1917* — Dog fumigated a second time, this time at 20° C. for a period of five hours.
Time when fumigation was begun, 2.45 p. m.
Time when fumigation was finished, 7.45 p. m.

Observations: As before, the animal remained quiet during the entire course of the experiment, and was taken from the tank apparently unharmed, and eating and drinking heartily.

*January 21* — No symptoms had appeared by morning. At 8 p. m., however, the animal exhibited an apparent stiffness in the hind legs. This passed off during the night, and no further symptoms were developed until on the morning of January 24, when a loss of coordination of the muscles of the hind legs was observed and the animal walked with a sprawling gait very similar to that shown by Dog I. Toward evening this condition was much more pronounced, and it persisted during the course of two days altho the animal developed no further symptoms.

*January 27* — All lameness was apparently gone, and recovery was complete.

DOG VI (FEMALE)

Weight of dog, 10.7 kilograms.

*October 27, 1916* — Dog fumigated at 25° C. for a period of three hours.
Time when fumigation was begun, 3.05 p. m.
Time when fumigation was finished, 6.05 p. m.

Observations: The animal remained quiet during the experiment and was removed from the tank in a perfectly normal condition. It ate heartily of roast beef. It had developed no symptoms by November 3.

*November 3, 1916* — Dog fumigated a second time, this time at 22° C. for a period of four hours and forty-five minutes.
Time when fumigation was begun, 3 p. m.
Time when fumigation was finished, 7.45 p. m.

Observations: The animal was removed from the tank apparently unharmed, and developed no symptoms during the night.

*November 4* — At 8 a. m. the dog was running about in a lively condition and was apparently normal. At 2 p. m., however, the animal was found in convulsions; the legs, particularly the hind legs, exhibited tetany and the muscles of the abdomen quivered violently. By 6 p. m. the convulsions had become even more pronounced, and the animal refused food and drink.

*November 5* — At 10 a. m. the animal was found with its body flexed to the left, and rigid; all the legs were rigidly extended; when an attempt was made to straighten the animal out, the head would crash violently against the floor and the animal would immediately return to its former position. At 2 p. m. the animal's condition had not changed and it was decided to attempt to relieve its condition by a blood transfusion. At 4 p. m. this operation was undertaken; the animal became anesthetized with ether very readily, and did not struggle on coming out of the anesthesia; approximately 200 mils of dark coffee-colored blood was drawn from the carotid artery of the poisoned animal, and 500 mils of defibrinated blood from a healthy dog was transferred thru the femoral vein. At 7 p. m. the animal was found in a stupor; the respiration was fairly regular. At 9 p. m. the respiration was very irregular and labored; at intervals of about one and one-half minutes there appeared incoordinated movements of the muscles of the diaphragm and the chest, each set working alternately with the result that no air was inhaled; these spasms lasted for from one-half to three-fourths of a minute, and at their height all the legs would move as if the animal were swimming, and would then become extended and rigid; the muscles of the abdomen would quiver, then the animal would give one or two deep gasps and regular respiration was resumed for a time but gradually became lessened in depth again until the incoordinated movements reappeared; an attempt was made to obtain a kymographic record of the respiration, but the animal became so active that this was impossible. At 10 p. m. the animal's condition was about the same, tho a slight improvement in the respiration was observed; the heart rate was 52, the respiration 30–40.

*November 6* — The animal seemed not to be greatly improved; the respiration was irregular, with a tendency to return to the type observed the day before, but it never reached that type again sufficiently to give a good record. At 12 m. the anal temperature was 26.8° C.; the animal urinated and passed very dark soft feces; the external anal sphincter was relaxed, but the internal sphincter was about normal; the respiration was regular but very weak; the animal made swallowing movements and was given a very little water, which was swallowed with difficulty. At 12.30 p. m. the animal was placed in a warm room (30° C.); the respiration was fairly regular but weak, and the animal gave occasional gasps. At 2.30 p. m. the external temperature was rather low and the room temperature was therefore increased; the dog's respiration was 48, and was regular but very shallow; the heart rate was 64 and was very regular. At 3 p. m. 1 milligram of strychnin sulfate was injected; the anal temperature was 30.5° C., the external anal sphincter was still relaxed. At 4 p. m. the respiration had improved to some extent, but it became shallow again at 4.30; the rate was about 50 a minute; the heart rate was 75. At 5 p. m. the animal was found gasping weakly; the heart rate was above 100. The animal died at 5.10, apparently as the result of respiratory failure; the sound of the heart indicated that that organ was in excellent condition. At 6 p. m. the body was opened; the general condition of the organs was found to be good; the spleen and pancreas were of a dark blue color; the peritoneum was slightly hyperemic; the stomach and the intestines were slightly hyperemic, with occasional hemorrhagic areas possibly due to roundworms which were present in large numbers; the rectum contained a small amount of soft, brown feces. There was no nystagmus observed in this case, nor did the pupils appear to be involved.

### DOG IX (MALE)

Weight of dog, ?. (The dog, which was a very small one, was not weighed. Its weight was probably about 3 kilograms, and it was completely free of excess fat. This dog had a severe Demodex infection.)

*December 4, 1916* — Dog fumigated at 22° C. for a period of five hours.
Time when fumigation was begun, 12.30 p. m.
Time when fumigation was finished, 5.30 p. m.

Observations: The dog appeared restless during most of the time it was in the fumigation chamber. At 1.30 p. m. it had vomited. At 5 p. m. it was observed to be unsteady on its feet; it staggered and fell, regained its feet, and fell again. At 5.30, when it was removed from the tank, the animal was able to walk but staggered about very much as if it had been intoxicated with alcohol; it ate cooked meat.

*December 5* — The animal was found lying on its side in a helpless condition; the tongue and the lips were cyanotic; the skin temperature was very low; the heart rate was 70, but was regular; the respiration was irregular, as if from disorganization of the respiratory center, and was difficult to count; the conjunctival reflex was good; the dog was unable to move its legs; tremors were observed in the leg muscles, the abdominal muscles, and the lips; the jaws moved incessantly, as if the animal was gasping for breath; the dog was placed in a warm room on a piece of cotton. The animal's condition remained unchanged during the remainder of the day; its respiration was always shallow and irregular. At 7 p. m. it was found dead. A post-mortem examination showed the following: heart distended and all the chambers filled with ante-mortem clots; these clots also appeared in the larger blood vessels; the stomach was very distended and was filled with gas and undigested food; the duodenum was filled with a sticky, bloody mucus; the jejunum contained a dark brown mucous substance; the blood was a trifle darker than normal.

In this case asthenia appeared to be the principal symptom. The action of the drug was rapid, but did not cause the type of convulsions described by Filehne as following a rapid action of the drug.

### DOG X (FEMALE)

Weight of dog, ? (medium-sized).

*December 7, 1916* — Dog fumigated at 20° C. for a period of seven hours and fifty minutes.
Time when fumigation was begun, 2.10 p. m.
Time when fumigation was finished, 10 p. m.

Observations: The animal remained quiet during the fumigation, and when removed from the tank at 10 p. m. it appeared entirely normal. No symptoms of poisoning appeared until two days later.

*December 9* — At 9 a. m. the animal was apparently normal. At 3 p. m. it exhibited a weakening of the hind legs, and walked with a staggering, sprawling gait, showing a lack of coordination of the muscles of the hind legs; it had recently vomited. At 5 p. m. the animal was no longer able to walk, and the extensors of the fore legs were in tetany. At 6 p. m. the animal was no longer able to stand; nystagmus had appeared, and both pupils were dilated, the left more widely than the right; the dog drank a little milk.

*December 10* — The general condition of the animal was about the same as on the preceding night. Nystagmus was slight. The dog drank milk and water in the morning, but refused both food and drink later in the day. The legs were extended; there was nothing definite about the extension of the legs, one or both of the hind legs sometimes being extended and rigid, and the fore legs sometimes being thus affected; at times the tetany would last for a long period, and again it would be of short duration. At times the head was drawn strongly backward, with the muscles of the neck rigid. The pupils reacted slightly to light. There was an odor of nitrobenzene on the animal's breath.

*December 11* — At 8 a. m. the general condition of the animal was worse, but it was still conscious; all the legs were rigidly extended for minutes at a time, and the head was drawn backward; when this condition passed off the animal was left prostrated; the pupils were contracted unequally. At about 1 p. m. the animal passed about 100 mils of dark urine (the first passed since the fumigation). At 10 p. m. the pupils were about normal; the animal swallowed a very little milk and water when these were placed in its mouth; when disturbed, the animal would attempt to use its legs, and this resulted in a tetanic convulsion involving the muscles of the legs and the neck.

*December 12* — During the night the animal passed about 100 mils of very dark urine (almost like black coffee). The animal had regained the ability to move its legs a little, tho an attempt to do so usually threw them into tetany of the type described above. At 11 a. m. the animal was found with all four of its legs in constant motion; these movements were fairly well coordinated and rapid, as in the act of running or swimming; they would increase in rapidity and violence until the animal was thrown into a convulsion which apparently involved every muscle of the

body; the legs were straight and the head was drawn down under the body between the hind legs; these spasms lasted for a few seconds, during which respiration ceased entirely; as the spasms passed off, the animal would give a short, hollow cry and resume the running movements, tho with evidence of exhaustion; both the heart rate and the respiration were rapid; if the animal was lifted up or its legs were held for a moment, the swimming or running movements would cease for a time; the excitement was very similar to postanesthetic excitement, except for the convulsive periods. At 3.30 p. m. the animal was found quiet and relaxed; the respiration was 35. At 5 p. m. the animal swallowed a little milk and water which were placed in its mouth. At 10 p. m. convulsions were observed which were of the opisthotonos type except that the muscles of the hind legs were relaxed; these convulsions appeared at intervals, and were induced if the animal was disturbed.

*December 13* — The animal was able to swallow but a very little liquid food when this was placed in its mouth, and so had had little or no nourishment. It lay on its left side, with its head drawn back on its body, its fore legs extended and rigid, and one or both of its hind legs drawn up to its body. The respiration was slow, 16–20, and was deeper than normal; the heart was irregular, the rate being about 160; the tongue and the conjunctiva were slightly cyanotic. Toward evening the heart seemed weaker; the animal swallowed a little milk; it had passed very little urine, and the little that was passed was of a dark color. The cause of the color of this urine has not been determined; it was not hematoporphyrin, by the spectroscopic test.

*December 14* — The animal was found dead. It died sometime after 11 p. m. of the preceding day. A post-mortem examination showed the following: lungs, hypostatic congestion of the left lobe; liver, congested and dark brown in color; esophagus and stomach, containing a little clear mucous substance; all other organs normal.

### DOG XI (FEMALE)

Weight of dog, ? (small, about 8 kilograms).

*January 5, 1917* — Dog fumigated at 20° C. for a period of three hours.
Time when fumigation was begun, 2.25 p. m.
Time when fumigation was finished, 5.25 p. m.

Observations: The animal remained fairly quiet during the fumigation and was removed from the tank at 5.25 p. m. in an apparently normal condition. It was lively, ate heartily, and showed no symptoms of poisoning. No symptoms developed during the next three days.

*January 8* — When seen at 11 a. m. the animal was apparently well and normal. At 5 p. m., however, it exhibited a loss of coordination of the muscles of the hind legs, and had vomited at some time previously. At 8 p. m. it was unable to stand.

*January 9* — The animal was found lying on its left side in a helpless condition; when placed on its right side, it struggled violently until it regained the left side; it refused cooked meat and water, but drank a little milk. At 12 m. nystagmus was observed; the pupils were normal; the animal ate a little cooked liver. By 3 p. m. nystagmus was very marked; the pupils were normal; knee-jerk reflex was good in both legs. When seen at 7 p. m. the animal tried to stand on its feet, but its hind legs were apparently paralyzed; when it did not succeed, it at once began to howl.

*January 10* — The condition of the animal was about the same. It lay continually on its left side and was unable to move its body. There was a certain amount of rigidity of the leg muscles at times, but this was not well marked. Knee-jerk reflex was good. The animal ate cooked meat, and drank milk but no water. Nystagmus was not noticeable.

*January 11* — The condition of the animal was slightly improved. It could move its legs a little. It ate meat and drank milk, but refused water (it was given meat and milk twice). The pupils were normal.

*January 12* — The condition of the animal was much improved. It was able to lift its body on its fore legs and crawl about the cage, but the fore legs weakened quickly. The animal passed urine which was very dark. It ate meat greedily and drank some water.

*January 13* — The condition was much improved. The animal was able to walk about very well, but its legs seemed weak and gave way at times.

*January 14* — The condition was still further improved.

*January 15* — The condition was apparently normal. The dog was turned loose with the other dogs.

In this case no definite convulsions were observed, the dominant symptom being paralysis such as was reported by Filehne as following a slow action of the drug.

DOG XVIII (FEMALE)

Weight of dog, ? (small, rather thin; heavy Demodex infection).

*April 23, 1917* — Dog fumigated at 23° C. for a period of four hours.
Time when fumigation was begun, 2 p. m.
Time when fumigated was finished, 6 p. m.

Observations: The animal was restless for a time after being placed in the fumigation chamber, but soon became quiet. It was removed apparently unharmed, and never developed any symptoms of poisoning as the result of this fumigation.

*May 16, 1917* — Dog fumigated a second time, this time at 20° C. for a period of five and one-half hours. (The dog was slightly fatter than when first fumigated.)

Time when fumigation was begun, 1.10 p. m.
Time when fumigation was finished, 6.40 p. m.

Observations: As before, the animal was a bit restless when first placed in the tank, but it soon became accustomed to its new environment and became quiet. It was removed from the tank apparently unharmed, showing no signs of nitrobenzene poisoning and drinking water freely.

*May 17* — No symptoms had developed.

*May 18* — The animal was found with its hind legs paralyzed, and there were evidences of its having thrashed about during the night. It drank milk and water freely and ate meat. It was placed in a padded cage.

*May 19* — The general condition of the animal was worse. It could raise its head and wag its tail, but its legs were useless. It ate and drank. This condition remained about the same until May 22, when some improvement was noticed.

*May 23* — The animal was found with its body raised on its fore legs, swaying from side to side, apparently making efforts to stand up but its hind legs were useless. The animal had not defecated since being placed in the cage, altho it was taken out several times for this purpose.

*May 24* — The animal was very much improved. It could use its fore legs very well and had some use of its hind legs, but when it attempted to walk it staggered and fell, or rather tumbled to the floor, striking its jaws against the floor with considerable force. It appeared very nervous, and was always moving and fidgeting about, apparently unable to remain quiet at all. The animal defecated for the first time since the beginning of the experiment.

*May 26* — The general condition of the animal was about the same. It was taken out on the lawn for exercise. In standing, its hind legs were spread far apart. It was unable to walk or to run, but it actually tumbled along, jumping high into the air and coming down on its head or its back, turning somersaults, or tumbling over sidewise. This dog was by nature playful and it had lost none of its playfulness as the result of the fumigation; its efforts to play always resulted in its throwing itself violently about. An interesting observation was the attempt of the dog to go toward any one when called; it made better progress in attempting to go in the opposite direction. It apparently was confused as to distances, and was wholly unable to make progress in a straight line.[10]

RABBITS I AND II, AND GUINEA PIGS I AND II

*November 2, 1916* — Animals fumigated at 22° C. for a period of nine hours.

Time when fumigation was begun, 10.30 a. m.
Time when fumigation was finished, 7.30 p. m.

Observations: These animals were apparently normal when removed from the tank, and never developed any symptoms afterward.

[10] This animal was killed in February, 1918, and a histological examination of the cerebellum revealed a striking absence of Purkinje cells. Only from 5 to 10 per cent of the number found in a normal dog were present. The contour of the cerebellum was apparently normal, and those Purkinje cells which were present were scattered fairly uniformly thruout the cerebellum. The condition of the animal had never improved very markedly; and while it had learned many new tricks regarding locomotion, its actions were always typically those of a cerebellar animal.

*November 18, 1916* — Animals fumigated a second time, this time at 24° C. for a period of nine hours and thirty minutes.
Time when fumigation was begun, 10 a. m.
Time when fumigation was finished, 7.30 p. m.

Observations: As before, these animals showed no effects of the drug, either during the fumigation or afterward.

RABBIT III AND GUINEA PIG III

*Dec. 22, 1916* — These animals were placed together in the fumigation chamber at 5.15 p. m., and were allowed to remain there until 4 p. m. on December 23. The temperature of the chamber remained constant at 20° C. during the first seven hours, then it gradually dropped until at the end of the next seven hours it was 15° C., and then it rapidly rose to 20° C. again. During the second seven hours no air was introduced into the tank.

Observations: The animals nestled together and remained quiet during the entire experiment. A string was tied to the rabbit's leg, and every hour or so the animal's reflexes were tested. They remained good. Both animals were a trifle stupid when they were removed from the tank. They were offered food and water, but would not drink and barely nibbled at the food. Suddenly the guinea pig fell on its right side and was unable to regain its feet. When placed on its left side, it immediately turned again to the right side. Violent tremors were observed in all its muscles, and presently it was seized with convulsions; all the legs were rigid and the head was drawn back on the body. This spasm lasted but a few seconds, and when it ended the animal shook itself violently and then executed running movements similar to those described in dogs. These movements were extremely rapid and lasted until another convulsion appeared. At 8 p. m. the guinea pig seemed to be recovering and was able to raise itself on its fore legs. It remained quiet for some time, and when observed the next morning it was dead. A post-mortem examination showed the lungs to be distended and the air passages were filled with blood; the blood was dark brown; the liver was congested; the other organs were normal.

At the end of two hours the rabbit had developed no symptoms, and at about 6 p. m. it was again placed in the fumigation chamber. The animal reacted to the jerk of the string until about 9 p. m. It was then removed

from the tank and was found to be in a stupor; it was wholly relaxed and perfectly reactionless. It remained in this condition for a few hours, and then died, without any signs of convulsions.

### GRAY RATS

(*Mus decumanus*).

Five young rats were placed together in a large wooden box having a capacity of 10 cubic feet. Fifteen drops of nitrobenzene were placed on a strip of cheesecloth and the cloth was suspended in the box, which was then closed for twelve hours. At the end of that time the rats were removed. The animals were all perfectly anesthetized, and three of them were reactionless. One died five hours later, and another was killed for the purpose of examining its blood; both of these had dark brown blood. All the other three exhibited either right or left rotatory (pinwheel) movements; one of them was seen to roll over and over for several feet before becoming exhausted. Two of these remaining three died without showing other symptoms, and one recovered (at least temporarily) and escaped.

Two adult rats of the same species were fumigated together in the regular fumigation chamber for three and one-half hours at a temperature of 23.5° C. When removed from the tank they were apparently unharmed. Both of these died two days later, probably from lack of nourishment since it was impossible to induce them to eat while in captivity.

### WHITE RATS

It was found that white rats could not stand a fumigation at ordinary temperatures for longer than from one and one-half to two hours. However, the rats used in these experiments were infected with trypanosomes and spirochætes, and this fact may have had something to do with hastening the action of the drug. The rats that were still alive when removed from the tank showed only paralysis and usually died very quickly.

### CAT X

*September 26, 1916* — Cat fumigated at 17° C. for a period of five hours.
Time when fumigation was begun, 11.50 a. m.
Time when fumigation was finished, 4.50 p. m.

Observations: The animal lay down and remained quiet for about three hours, and then became restless for a time but soon became quiet again. When first removed from the tank the animal appeared well and started to walk away, but lost control of its hind legs and tumbled about for a moment, then became excited. It vomited (chunks of meat which had not started to digest), and then lay prostrate for about one-half hour. The lips and the tongue were cyanotic; the pupils were dilated and did not react to light. The animal's condition improved shortly and it again appeared well. On the following morning a quantity of sticky, bloody feces was found in the animal's cage; no further symptoms of poisoning had developed, however, nor did any symptoms appear during the next four days. At the end of this time the cat was found dead.

CAT XVIII

*October 5, 1917* — Cat fumigated at 22.5° C. for a period of three hours.
Time when fumigation was begun, 9 a. m.
Time when fumigation was finished, 12 m.

Observations: The animal remained quiet during the fumigation and was removed from the tank apparently unharmed, but became slightly stupid toward evening. A sample of blood was taken and examined. It was dark brown and showed methemoglobin by spectroscopic analysis.

*October 6* — The animal was found with well-advanced symptoms of nitrobenzene poisoning — nystagmus, paralysis of the muscles of the hind legs, and periods of excitation followed by prostration. The cat refused milk, nor was it possible to place any in its mouth. A sample of blood drawn from the ear was coffee-colored and showed the same spectrum as on the preceding day.

*October 7* — The condition of the animal remained about the same. It lay on its side entirely helpless and apparently unconscious.

*October 8* — The condition gradually grew worse and the animal died toward evening. A post-mortem examination showed a pronounced congestion of lungs and viscera, and the blood vessels of the neck were turgid with blood.

HEN V

*March 21, 1917* — Hen fumigated at 30° C. for a period of six and one-half hours.
Time when fumigation was begun, 1 p. m.
Time when fumigation was finished, 7.30 p. m.

Observations: The bird was removed from the tank apparently normal except that it appeared a little stupid. The feces were formed when the bird was first placed in the fumigation chamber, but those deposited immediately after the bird was removed from the tank were soft, stringy, and slightly bloody.

*March 22* — The bird appeared normal except that the neck feathers were constantly ruffled — a condition which induced such a belligerent attitude on the part of the other birds in the cage that this hen had to be placed by itself. No further symptoms developed until March 27, on which day the bird was found lying prone on its side and apparently unable to stand. When the bird was lifted it exhibited a circular rotation of head and neck; and when it was placed on its feet, the legs stiffened, throwing the bird backward.

*March 28* — The bird's general condition was about the same. Nothing new was especially noted.

*March 29* — The bird's condition had grown worse. The skin was cold, and the bird was placed in a warm room. There appeared frequent periods of excitation, during which the bird thrashed about a good deal.

*March 30* — The bird was found lying on its left side, with its left leg extended and rigid and its right leg exhibiting violent tremors. The respiration was normal. The head was moving by jerks sidewise. When placed on its feet the bird lunged forward instead of backward. At 2 p. m. the bird swallowed some water when its head was placed in water and then released; it also swallowed a little moistened bread when this was placed in its mouth. Each attempt at swallowing was followed by excitation, during which the head was drawn back rigidly between the wings or revolved slowly, describing broad circles. When placed on its feet the bird lunged backward.

*March 31* — The bird was again fed as described.

*April 1* — The condition was about the same, altho the bird appeared stronger. When placed on its feet it attempted to walk, but the legs stiffened and the bird was thrown forward.

This bird never fully recovered. It was able to squat on its feet after a time, but refused to walk; when urged, it took two or three rapid steps and then tumbled over forward. It was unable to remain on a perch, falling either forward or backward. The wing movements were well coordinated. For a long time the bird was unable to eat without assistance, but it was finally taught to do so. The bird was killed on June 11, in order to make an examination of the brain tissues.

HEN VI

*March 22, 1917* — Hen fumigated at 27–28° C. for a period of eleven hours.
Time when fumigation was begun, 10 a. m.
Time when fumigation was finished, 9 p. m.

Observations: The bird was removed from the tank apparently unharmed. The feces were as described for Hen V.

*March 23* — The bird was apparently well, but not very active. It ate cracked corn and drank water. The neck feathers were ruffled.

*March 24* — When first seen on this day (at 8 a. m.) the bird appeared normal. It was taken from the cage and placed on the floor. It was able to walk and run very well, but suddenly showed a tendency to give way to the left side; it flew to a perch 18 inches high, but was unable to retain its position; it fatigued very easily. At 10 a. m. the attendant reported that the bird had been in convulsions; it appeared normal except that it was a little dull. At 3 p. m. the bird appeared to be drowsy; it was removed from the cage and placed on its feet; it stood swaying from side to side; when it attempted to walk, it staggered and then swayed backward, taking several steps in an effort to catch itself; after this excitement its head was bent back between its wings. At 4 p. m. the bird was found lying on its side and was unable to stand; when it was picked up, its head rotated in a circle, sweeping the back and the wings. At 4.15 about an ounce of clear fluid came from the bird's mouth. At 5 p. m. periods of excitation were observed; the legs were in violent motion as in the act of running, and the head shook violently as if the bird were

trying to dislodge something in it; these periods of excitation were of short duration and were followed by periods of prostration lasting for several minutes, during which the muscles were wholly relaxed and the neck was limp; then with a sudden jerk, the period of excitation would appear again; this excitation could always be elicited by disturbing the bird; when the bird was placed on its feet, the legs stiffened and threw the body backward; the legs were bluish (they were pink normally); frequent movements of the gullet were observed, these movements often involving the mouth. At 5.15 another ounce of clear fluid came from the mouth. At 6 p. m. the bird made a violent effort to regain its feet; the wing movements were well coordinated but weak; this effort was followed by excitation during which the legs moved violently as described above.

*March 25* — At 9 a. m. the bird's condition was worse; there was constant rotation of head and neck; convulsions occurred as before; when placed on its feet, the bird squatted quietly for a moment and discharged a large quantity of watery fluid from the anus, and then went into convulsions again. At 5 p. m. the bird was apparently better, and was resting quietly in an upright position. At 7 p. m. the bird was found in convulsions; the head was bent firmly on the venter (almost between the legs); the bird had no control of any muscle.

*March 26* — In the morning the bird was found with all muscles relaxed except the neck muscles, which were rigid and held the head firmly against the venter. At 6 p. m. the bird was found dead. A post-mortem examination revealed a strong odor of nitrobenzene in all the organs; the crop and the gizzard were filled with cracked corn, which had not started to digest altho the bird had had nothing to eat during the preceding sixty hours: the other organs were about normal.

HEN VII

*March 25, 1917* — Hen fumigated at 25° C. for a period of eight hours.
Time when fumigation was begun, 2.15 p. m.
Time when fumigation was finished, 10.15 p. m.

Observations: When removed from the tank the bird was a trifle stupid but was otherwise normal. It developed no symptoms of poisoning until March 30.

*March 31* — The bird showed symptoms very similar to those described for Hen VI.

*April 1* — The bird was found dead.

On March 27 (two days after the fumigation) this hen laid an egg. The egg was opened on March 29; a strong odor and a very characteristic taste of nitrobenzene were detected in the yolk, but the white did not contain more than a trace of the chemical. This phenomenon can easily be explained by the fact that nitrobenzene is soluble in fats, but is scarcely soluble at all in the white of eggs.

HEN VIII AND ROOSTER III

*May 10, 1917* — Birds fumigated together, at 23° C., for a period of eight hours.
Time when fumigation was begun, 2 p. m.
Time when fumigation was finished, 10 p. m.

Observations: The rooster was found dead at the end of the fumigation period. The hen appeared slightly stupid when removed from the tank and became easily fatigued, but was otherwise normal. No further symptoms developed in the hen until on May 14, when it was seen to stagger on attempting to run. During the next few days the bird was very stupid. It did not eat much, staggered in attempting to walk, and fatigued easily.

*May 25* — The condition of the bird was apparently normal again. No further symptoms ever developed in this bird.

PIGEONS IV AND V

*June 11, 1917* — Birds fumigated at 24° C. for a period of six hours.
Time when fumigation was begun, 1.10 p. m.
Time when fumigation was finished, 7.10 p. m.

Observations: The birds were apparently normal when removed from the tank. They could fly and run easily.

*June 12* — One of the birds showed the following symptoms: it was unable to fly, tho the wing movements were fairly well coordinated; in attempting to walk, it lunged forward and tumbled on its head; there was rotation of head and neck.

*June 13* — The bird showing on June 12 the symptoms described, flew the length of the room along the floor, its head touching the floor. It probably had the use of its wings but could not direct the flying movements. The other bird showed symptoms of poisoning on this day. Both the birds were killed about noon, and the nervous tissues were fixed as described earlier (page 429).

## OBSERVATIONS OF THE ACTION OF NITROBENZENE ON INSECTS

During the fumigation of the animals a number of external parasites dropped from the hosts. These were collected at the end of the fumigation period and observations were recorded regarding the action of the drug on them. Some of these observations were as follows:

### FLEAS

Eighty-three fleas of the genus Ctenocephalus were recovered from the bottom of the tank after the fumigation of Cat X (fumigated for five hours at 17° C.). Most of these began to show signs of life in about one and one-half hours; they were put into a glass tube and placed in a warm room, and in about twelve hours all the fleas had recovered with the exception of about one-half dozen, which were stuck fast to the tube.

Nineteen fleas of the same genus were recovered in a stupefied condition from the bottom of the tank after the fumigation of Dog I (second fumigation, six hours at 23° C.). Three of these showed signs of life, and most of them recovered during the next twelve hours.

Seventy-six fleas of the same genus were recovered from the tank after the fumigation of three kittens for a period of four hours at 22° C. Some of these fleas showed signs of life when removed from the tank, and twenty of them recovered and lived for several days.

### BITING LICE

A large number of biting lice (*Trichodectes subrostratus*) were recovered in a stupefied condition from the bottom of the tank after the fumigation of Cat X (fumigated for five hours at 17° C.). Nearly all of these recovered during the next twelve hours.

A large number of the biting lice of poultry (*Menopon gallinae*, *Menopon stramineum*, *Lipeurus heterographus*, and *Goniocotes gigas*) were recovered

from the tank after the fumigation of Hen V (fumigated for six and one-half hours at 30° C.). The lice were all apparently dead, showing no signs of life, at the end of twelve hours. At the end of eighteen hours, however, some of them were seen to be moving their legs. In Goniocotes these movements were rapid, and were very similar in character to the movements of the legs of poisoned guinea pigs.

Approximately three hundred biting lice, representing six species, were recovered from the tank after the fumigation of a chicken for a period of one and one-half hours at 20° C. Some of these insects showed signs of life when removed from the tank, and nearly all of them recovered entirely during the next few hours.

Nineteen specimens of biting lice were recovered from the bottom of the tank after the fumigation of Hen VI (fumigated for eleven hours at 27–28° C.). None of these showed signs of life when taken from the tank, and none recovered.

### THE FOLLICULAR MITE

### (*Demodex folliculorum*)

Two or three cases of mild infection of demodecic scabies in dogs apparently cleared up after fumigations for long periods at low temperatures. One of these cases was Dog V, which was fumigated twice — once for twelve hours at 20° C., and once for five hours at 20° C. These observations led to the following experiments for the purpose of determining the value of nitrobenzene in controlling demodecic scabies.

A special fumigation chamber was constructed in such a way that the animal's nose passed thru a rubber collar and remained on the outside of the chamber, and an attempt was made to fumigate the body of the animal without permitting it to inhale a large amount of the vapor. Morphine and chloral hydrate were given in order to cause the animal to remain quiet during the fumigation. A six-hour fumigation under these special conditions had no effect on the mites, nor was it possible to induce dogs to remain quiet without giving them large doses of the narcotics. The method was therefore abandoned.

Small pieces of skin heavily infected with *D. folliculorum* var. *canis* were placed in a petri dish in which there was a drop or so of nitrobenzene. The dish was then kept at a temperature of 30° C. for six hours. At the end of that time the mites were still alive.

It was observed that a 33-per-cent solution of nitrobenzene in olive oil would have no apparent effect on dogs if applied externally and if the animal was allowed to remain in the open air, in spite of the fact that an external application of a solution of this strength invariably killed cats and rabbits. Hence a small, short-haired dog [11] having a heavy infection of *Demodex folliculorum* was bathed thoroly and frequently with the 33-per-cent solution; but no improvement in the condition of the animal could be noticed.

## OBSERVATIONS OF THE ACTION OF NITROBENZENE ON INTERNAL PARASITES

### GAPEWORMS

### (*Syngamus trachealis*)

Three chicks showing symptoms of gapes were fumigated together for two hours at 25–26° C. on June 23, 1917. Two of the chicks developed symptoms of nitrobenzene poisoning on June 24. One of these died on June 25 and the other on June 26. Two nearly mature pairs of *Syngamus trachealis* were recovered alive from the trachea of the former, and three living pairs were taken from the trachea of the latter. The third chick developed typical symptoms of nitrobenzene poisoning on June 26. By July 8, however, this chick had fully recovered from the effects of the drug, and it had also recovered from the gapes by July 8. The recovery from the gapeworms, however, cannot be attributed to the action of the drug on the worms, since with its improved environment it would in all probability have recovered anyway.

### INTESTINAL WORMS

A number of roundworms (*Belascaris marginata*) were found in the feces of Dog III on the morning following a fumigation for five hours at 18° C. These worms were observed to be dead and their death was attributed to the action of the drug. However, roundworms of the same species were recovered, very much alive, from the intestines of nearly all the dogs examined, even in cases following long periods of fumigation.

[11] The solution was not tried on long-haired dogs, nor was a stronger solution tried. The animal did not lick the solution off, presumably because of the burning taste of nitrobenzene.

### COCCIDIA

Specimens of *Eimeria avium* in the oöcyst stage were recovered from the feces of Hen VII. These oöcysts appeared normal, and the development of sporocysts and sporozoites occurred as usual.

## EXPERIMENT TO DETERMINE THE ACTION OF NITROBENZENE ON DIGESTIVE FUNCTIONS

Post-mortem examinations of animals poisoned by nitrobenzene usually revealed the fact that food which had been in the stomach for some days had not started to digest. A special experiment was therefore conducted in order to check these observations.

At 11 a. m. on October 3, 1916, four kittens, all from the same litter, were each given an equally large portion of boiled hamburg steak. At 11.10 three of these kittens were placed in the fumigation chamber, where they were fumigated for four hours at a temperature of 22° C.

At 2.20 p. m. (three hours and ten minutes after the fumigation was begun) one of the animals died. The other two were removed from the tank at 3.10 and showed well-advanced symptoms of poisoning. One of them died at about 4 p. m. and the other at about 5 p. m.

At about 5.30 p. m. the control kitten was killed with chloroform and a post-mortem examination was made of all four animals. The stomachs of the animals that had been fumigated contained the full amount of the hamburg steak eaten, and in no case had it even started to digest. The digestion of the hamburg steak in the stomach of the control animal was well advanced.

## EXPERIMENTS TO DETERMINE THE ACTION OF NITROBENZENE ON BLOOD

### BLOOD COUNTS

Two pups, from the same litter and about three months old, were kept under similar conditions,[12] and blood counts were made on each for several days in order to determine the normal counts. Each animal was then fumigated, on different days and for different periods of time, and the blood counts were continued. Always, of course, as soon as an animal developed pronounced symptoms of poisoning it refused food, and this interfered with exact comparisons. The results of these experiments are indicated in the following tables:

[12] These animals were fed twice a day, each receiving at a meal 40 grams of cooked liver, ½ pint of milk, 50 grams of bread, and all the water it wanted.

DOG C (MALE — WEIGHT 2.7 KILOGRAMS)

| Date of blood count (1917) | Red blood-cells (per cubic millimeter) | White blood-cells (per cubic millimeter) | Hemoglobin (per cent) |
|---|---|---|---|
| January 10 | 5,196,000 | 23,400 | 60 |
| 11 | 5,312,000 | 25,000 | 60 |
| 12 | 5,344,000 | 14,000 | 65 |
| 13 | 5,336,000 | 15,000 | 60 |
| 14 | 5,040,000 | 16,000 | 64 |
| 15 | ..... | ..... | ..... |
| 16 | 4,936,000 | 11,600 | 62 |
| 17 | 5,178,000 | 17,400 | 60 |
| 18* | 5,472,000 | 16,600 | 63 |
| 19 | 5,496,000 | 16,860 | 62 |
| 20† | 5,500,000 | 17,200 | 66 |
| 21 | 5,608,000 | 23,600 | 62 |
| 22 | 6,040,000 | 19,620 | ‡72 |
| 23 | §7,144,000 | 24,400 | 80 |

* Dog fumigated for five hours at 20° C. on this date.
† Symptoms of poisoning appearing.
‡ The comparison standard was the methemoglobin standard, so that if methemoglobin is formed within the red blood-cells, as Roth claims, and these cells increase, it is not surprising that the percentage of hemoglobin also should increase.
§ Since the animal refused water and could be induced to take only a very little milk, it is probable that the rise in the red-blood-cell count was due to a concentration of the blood resulting from lack of water.

A microscopic examination of the blood of this dog showed that the erythrocytes were slightly distorted; they appeared loose and sac-like, and would not form rouleaux in fresh mounts.

DOG D (MALE — WEIGHT 2.5 KILOGRAMS)

| Date of blood count (1917) | Red blood-cells (per cubic millimeter) | White blood-cells (per cubic millimeter) | Hemoglobin (per cent) |
|---|---|---|---|
| January 10 | 4,904,000 | 15,720 | 65 |
| 11 | 5,604,000 | 19,660 | 65 |
| 12* | 5,296,000 | 14,660 | 66 |
| 13 | 4,600,000 | 12,660 | 65 |
| 14 | 5,446,000 | 14,060 | 66 |
| 15 | 5,000,000 | 11,200 | 64 |
| 16 | 5,040,000 | 11,860 | 62 |
| 17 | 4,798,000 | 12,740 | 62 |
| 18 | 4,712,000 | 11,660 | 60 |
| 19 | 5,024,000 | 11,600 | 58 |
| 20 | 4,974,000 | 11,200 | 85 |

* Dog fumigated for four hours at 20° C. on this date.

This animal showed a slight drop in the red-cell count on the day following the fumigation, but this was not sufficiently great to be of any importance. The animal developed no very pronounced symptoms of poisoning. Dog C, on the other hand, did develop pronounced symptoms, and died on the evening of January 23; but Dog C had been fumigated for four hours at 18° C. on December 12, 1916, as well as for five hours in this experiment. As the result of the first fumigation, however, the animal was apparently unharmed, nor was there any change in the blood counts following the first fumigation.

### SPECTROSCOPIC EXAMINATION OF THE BLOOD OF ANIMALS POISONED BY NITROBENZENE

A cat was fumigated for a period of three hours at a temperature of 23.5° C. Shortly after the fumigation a sample of blood was taken, diluted with distilled water, and examined spectroscopically. When the concentration was just sufficient to cause the oxyhemoglobin bands to disappear, a distinct band appeared between C and D, apparently in the exact position of the absorption band of methemoglobin. When the sample of blood was sufficiently dilute to cause the oxyhemoglobin bands to stand out clearly, the absorption band between C and D disappeared or was very faint. The undiluted blood was coffee-colored, and the diluted blood had the appearance of methemoglobin blood.

A young dog, a cat, a rabbit, a guinea pig, a chicken, and a pigeon were placed together in the fumigation chamber and fumigated for a period of three hours at 22.5° C. At the end of the fumigation, a sample of blood was taken from each and examined spectroscopically. The cat's blood showed the above-described band faintly; the guinea pig's blood showed the band very distinctly; the samples from the other animals failed to show the band. On the following day, blood samples were again taken and examined. The sample from the cat showed the band more markedly than on the preceding day; the sample from the guinea pig did not show the band at all, nor did the samples from any of the other animals.

A sample of blood was taken from a healthy cat and diluted with about fifty volumes of distilled water. The diluted blood was then shaken in

a test tube with a few drops of nitrobenzene. When examined spectroscopically, the sample showed no trace of the band, but only oxyhemoglobin. The sample was allowed to stand overnight, but the band even then failed to appear. Another sample was taken, diluted as before, and shaken with nitrobenzene. It was then placed in an incubator at a temperature of from 37° to 38° C. The methemoglobin band, above described, made its appearance at the end of four hours. However, since no control sample was incubated at the same time, this test is not a positive proof that nitrobenzene can form methemoglobin in blood outside of the animal.

The results described above agree fairly well with the findings of Filehne and others. There has been some disagreement regarding the nature of the band in question; however, a sample of methemoglobin prepared in the laboratory showed an absorption band in exactly the same position as that occupied by the "nitrobenzol band."

## HISTOLOGICAL EXAMINATION OF THE TISSUES OF ANIMALS POISONED BY NITROBENZENE

### DOGS

Four half-grown dogs, all from the same litter, were kept as nearly as possible under the same conditions. On January 24, 1917, three of them (Dogs E, F, and G) were placed together in the fumigation chamber and fumigated for a period of five and one-half hours at a temperature of 20° C. They were removed from the tank at 10 p. m., apparently unharmed.

On January 25 Dog F showed a slight lameness, hid himself away in a dark box, and did not eat well. The other two animals were apparently normal.

On January 26 all three of the dogs were found to have developed pronounced symptoms of nitrobenzene poisoning. The symptoms were of the same general character in each, but were more advanced in Dog F. All the animals were able to crawl about; they had a partial use of the fore legs but were not able to use the muscles of the hind legs. The knee-jerk reflex was good in each of the animals. There appeared an incoordination of the muscles of the neck, but there were no signs of

nystagmus, of abnormal pupil reactions, nor that the animals had vomited. All the animals drank milk, and Dogs E and G ate some meat.

On January 27, at 8 a. m., Dog F was found completely paralyzed except for slight movements of the hind legs, and there was a copious secretion of saliva. The knee-jerk reflex was good in both legs. At 9.30 a. m. this animal was howling excitedly. When disturbed it went into respiratory convulsions similar to those described for Dog VI (page 437). The animal was killed at noon and its tissues were fixed according to the methods described earlier (page 429).

Dog E refused food and water on this date, was wholly helpless, and howled incessantly. At 3 p. m., three hours after Dog F was killed, this animal was killed and its tissues were fixed in the manner described.

Dog G took milk in the morning on this date, but refused it at night. It exhibited the running movements of the legs described for Dog X (page 440), and howled a good deal.

On January 28 intense excitement was shown by Dog G. Its legs were moving rapidly with the running movements already mentioned. These movements continued for long periods at a time, and then the leg and the abdominal muscles would stiffen in violent convulsions; the head thrashed about and the animal gave guttural sounds as if worrying a rat; finally the animal would grasp part of its bedding with its teeth and hold it firmly for a moment, during which time respiration would cease, and then, after a few gasps, the running movements would begin again. At times the animal shook its head vigorously, as if trying to get rid of something in its ear. This dog and the control, Dog H, were killed in the course of the morning and their tissues were fixed, as nearly as possible, after the same manner as were the tissues of Dogs E and F.

Corresponding pieces of tissue from the different levels of the central nervous system of each of the four animals were carried thru the same fluids, and were finally stained and mounted on the same slide, as described on page 430.

No histological changes could be observed in the cells of any part of the central nervous system, except in the Purkinje cells of the cerebellum. The changes in these cells were typically chromatolytic degenerations.

## PLATE VI

1–4, Photomicrographs of Purkinje cells from the cerebella of four dogs of the same litter. x 525

1, Normal cells from control animal. The presence of tigroid bodies (Nissl bodies [N]) is to be noted

2, Cell from animal poisoned by the vapor of nitrobenzene, showing the first stages of chromatolytic degeneration. The much swollen cell-body, and the absence of tigroid bodies except a few in the vicinity of the nucleus, are apparent

3, Cells from animal poisoned by the vapor of nitrobenzene, showing (a) the swollen cell-body and the absence of tigroid bodies, and (b) a homogeneous appearance of the cytoplasm and the absence of tigroid bodies

4, Remains of a Purkinje cell which has undergone chromatolytic degeneration. (From the cerebellum of a dog poisoned by the vapor of nitrobenzene)

5–6, Photomicrographs of motor cells from the ventral horn of the cervical cords of two dogs from the same litter. x 525

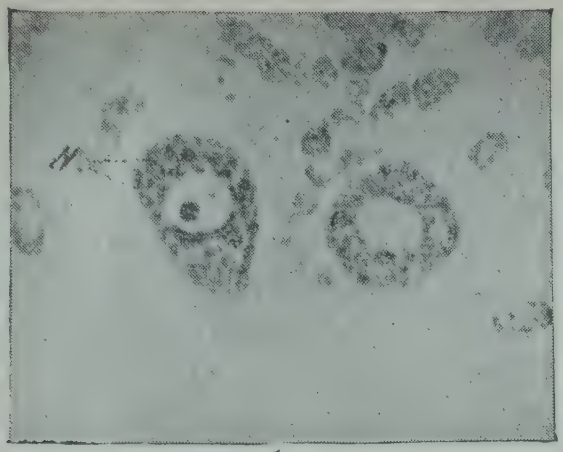
5, Normal cell from control animal

6, Cell, apparently normal, from animal (Dog F) poisoned by the vapor of nitrobenzene

7–8, Photomicrographs of sections thru similar convolutions of the cerebella of two dogs. x 60

7, From control animal, showing the presence of Purkinje cells (P) and a normal cortical area (c)

8, From animal killed nine months after being poisoned by the vapor of nitrobenzene (Dog XVIII), showing the absence of Purkinje cells and a much atrophied cortical area

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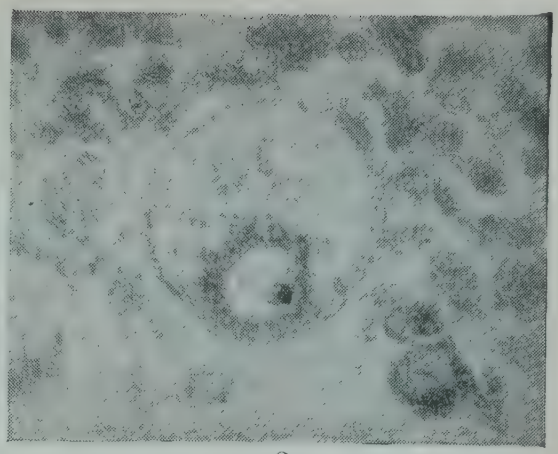

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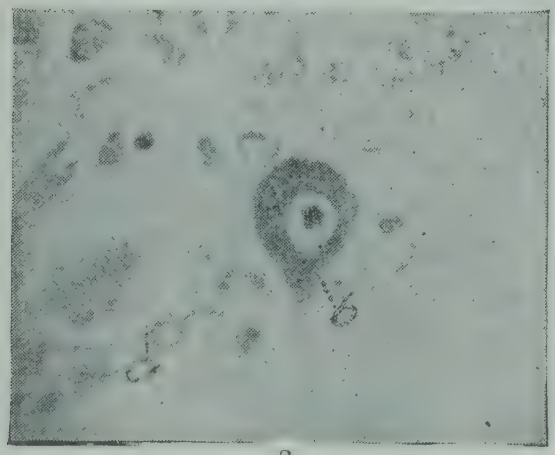


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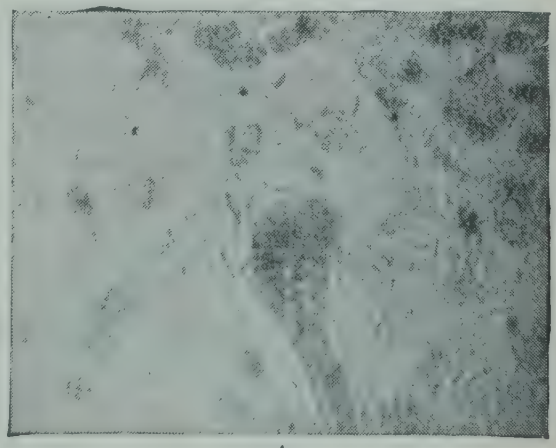

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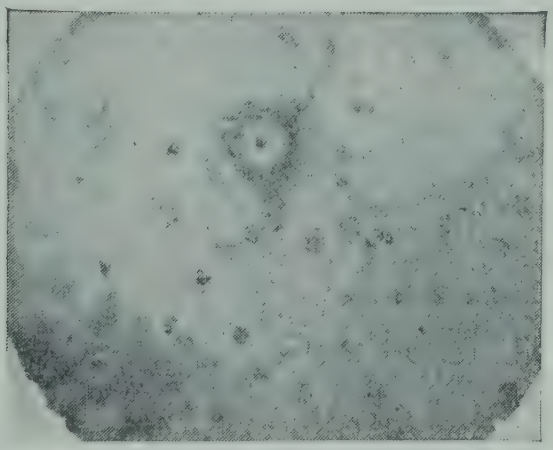

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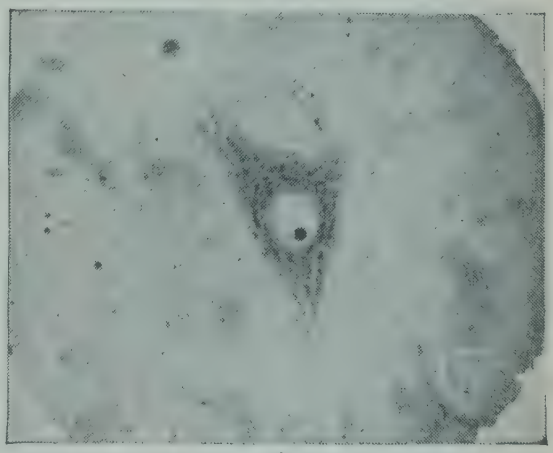

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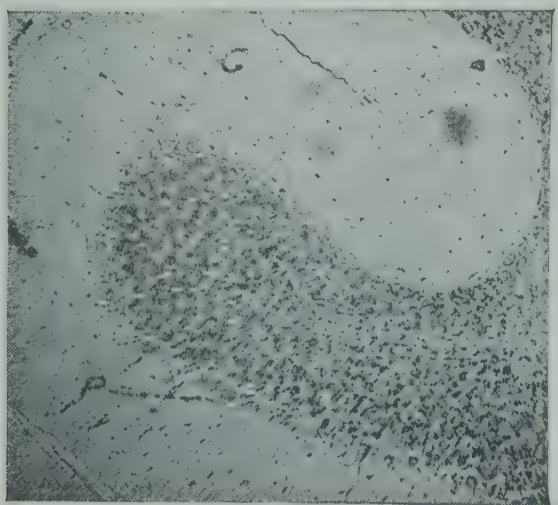


7

8

The Purkinje cells from Dog F (Plate VI, 2) were greatly swollen, and the Nissl bodies (tigroid bodies) were almost entirely absent. There was no stainable substance near the periphery, and that around the nucleus was massed and indefinite. Some of the Purkinje cells from Dog E were like those from Dog F; others were very much shrunken, about one-half "normal" size, and the whole was a darkly stained, indefinite mass with the nucleus almost obliterated. The Purkinje cells from Dog G were all very much shrunken (Plate VI, 4), and no Nissl bodies were to be seen. There was a small amount of stainable substance, massed and clinging about a much-shrunken nucleus. In many cases the nucleus had disappeared, and in numerous instances the entire cell seems to have disappeared. The Purkinje cells from the control animal, Dog H, were all apparently normal, the tigroid bodies staining excellently (Plate VI, 1).

The above experiment was repeated, and this time two controls were used instead of one. One of the poisoned animals was killed shortly after the first appearance of the symptoms, and only a few of the Purkinje cells from this animal showed degeneration. Another one of the animals was killed before the symptoms were very far advanced, and in this case but few of the Purkinje cells looked wholly normal and some of them showed definite chromatolytic degeneration. The third poisoned animal was killed after the symptoms were well advanced, and the cells from this animal had become so thoroly degenerated that there was scarcely anything left of them but irregular blotches. The Purkinje cells from the control animals were all apparently normal.

Sections were made, stained, and mounted on the same slide, of the following additional tissues from the control animals and from the animal in this later experiment in which the symptoms of poisoning were well advanced: liver, spleen, thyroid, adrenal gland, duodenum, and rectus femoris muscle. No signs of degeneration could be observed in any of these tissues, but there appeared to be a slight hyperemia of the liver, the duodenum, and the rectus femoris muscle; these tissues were dissected out before the infiltration of the saline solution, so that the blood remained in them.

### BIRDS

Two pigeons were fumigated with nitrobenzene, and when the symptoms became pronounced, they, together with a control, were killed by clipping

off their heads. The cerebellum was hurriedly dissected out and small sections from different parts were placed directly into the fixing fluid. The remainder of the technique was the same as that employed in the case of the dogs. The same degenerative changes in the Purkinje cells were found as were found in the case of the dogs. The Purkinje cells from the control bird were normal.

Two chickens, poisoned and killed in the same manner, showed the same type of degeneration in the Purkinje cells as is described above, while the cells from the control bird, stained and mounted on the same slide with those from the poisoned bird, were apparently normal.

### THE SYMPTOM COMPLEX OF NITROBENZENE POISONING

Unlike Letheby and Filehne, the writer has been unable to divide the symptom complex of nitrobenzene poisoning into two types — that accompanying a rapid action of the drug, and that accompanying a retarded action. As a matter of fact, the symptoms are never sufficiently uniform in any case, whether the action is slow or rapid, to permit of classification into types. There is a probability, however, that the symptom complex may be somewhat different in widely separated groups of animals; but this can be determined only by a summation of all the symptoms observed in experiments on a large number of individuals from each group.

So far as has been observed by the writer, the dominant symptom in frogs and in insects is a general depression, tho in insects a tremulous movement of the legs has also been observed. In birds and mammals, one or more or all of the following symptoms may appear in acute cases of poisoning by the vapor of nitrobenzene: cyanosis, nausea, vomiting, ataxia, asynergia (distinguished from other types of cerebellar ataxia in that there appears a retro- or propulsion in an antero-posterior plane instead of a lateral, the legs appearing as if either running away from the body and throwing the animal backward, or failing to keep up with the body and throwing the animal on its head), impairment of digestive functions, nystagmus, equal or unequal dilation or contraction of the pupils, irritability, tenderness of the occiput (headache), unconsciousness, hallucinations, adiadochokinesis, slowing of the pulse rate, irregular and weakened respiration, palpitation of the muscles, rapid (running) movements of the legs, rotation of the head and neck describing broad circles, rotation of the body around its longitudinal axis, asthenia, and the nitro-

benzene breath. In chronic cases the symptoms which persist are: asthenia, ataxia, and (described in man) anemia, malnutrition, and Korsakoff's psychosis.

### INTERPRETATION OF THE SYMPTOMS NAMED

While there is scarcely a single one of the symptoms described above that may not be referred to disorders of the central nervous system, still there is no doubt that nitrobenzene exerts a more or less serious local action on other tissues. The cyanosis observed in most cases of acute poisoning is undoubtedly due to a direct action of nitrobenzene on the blood; the blood has a dark brown color, and the presence of methemoglobin is demonstrable, at least in some cases, by spectroscopic analysis. Just how the changes in the blood are brought about is not definitely understood. Roth (1913) thinks that the nitrobenzene is converted into paraminophenol and that the latter drug acts on the red blood-cells, forming intracellular methemoglobin; he found no methemoglobin in the serum of certrifugalized blood. Türk (cited by Adams, 1912) says that not only is there a forming of methemoglobin, but there is also a destruction of the erythrocytes, due, he thinks, either to intravascular hemolysis or to a hyperfunctioning of the blood-destroying organs. That methemoglobin is formed, in certain cases, was demonstrated by the writer's experiments; the writer was unable, however, to demonstrate the destruction of erythrocytes, altho some morphological alterations of these cells were apparent. Also, Filehne (1878) has shown that nitrobenzene has a direct action on the muscle substance, causing the muscle to contract in rigor mortis; even the heart muscle was affected, according to him. Certain it is that nitrobenzene has an irritating action on the tongue and the mucosae; and, since it passes unchanged readily from the blood to other tissues, it is not impossible that it may have an irritating action on the deeper tissues also. However, if the symptoms produced are due to a direct action of the drug upon the blood, why, then, should there be such a long latent period in most cases? Furthermore, if the symptoms are due to a direct action of the drug upon muscles, glands, or abdominal organs, then these tissues should show histological changes; but the writer has failed to find anything more severe than a slight hyperemia, the cause of which may be easily explained on the basis of the hyperactivity of the organs concerned.

*Disturbance of digestive functions*

The retardation, or in some cases even the cessation, of digestive processes in the poisoned animals is not wholly understood. Casper (1859) observed that in post-mortem examinations of animals poisoned by nitrobenzene the stomach contents were always alkaline; and, since the acidity of the fluid in the stomach, especially in the pyloric end, has been shown to be essential to gastric digestion (Howell, 1918), it is possible that nitrobenzene in some way hinders the formation or secretion of hydrochloric acid.

*Cerebellar disturbances*

Turning now to the evidence indicating cerebellar involvement, the following facts may be noted. From the descriptions it will be seen, as already stated, that there is scarcely a single one of the symptoms appearing in cases of nitrobenzene poisoning that cannot be referred to disturbances in the cerebellum or the cerebellar paths, barring those which are undoubtedly due to a direct action on the blood. Moreover, this conclusion appears to be borne out by histological data, since the cerebellum is the only organ in which definite histological changes were found.

*Nausea and vomiting.*— Nausea and vomiting, accompanied by some of the symptoms named above, may be due to disorders of the cerebellar paths (Jelliffe, 1913). Nausea and vomiting may appear during the fumigation process, altho the animal may show no other pronounced symptoms for several days; but this does not preclude the possibility that nausea and vomiting are the result of the action of nitrobenzene on the cerebellum, since it is possible that a sufficient amount of the drug may be concentrated in the cerebellum to cause these first symptoms without enough being present to produce any further symptoms; moreover, if the animal were left in the fumigation chamber for a little longer period, the other symptoms would appear very quickly. If the cause of the vomiting were to be ascribed to a peripheral action of the drug, then the same explanation would have to be given as for the cause of the vomiting after the latent period, it would seem.

*Ataxia.*— The type of motor ataxia exhibited by animals poisoned by nitrobenzene, especially by dogs and birds, is typically cerebellar.

This is indicated by the hobble or sprawling gait in walking, the position of the legs in standing, and other characteristics mentioned heretofore (page 462).

*Adiadochokinesis.*— Adiadochokinesis is, perhaps, the best interpretation of the type of convulsions observed. This is a term originally used by Babinski to describe a peculiar type of incoordination in patients (Jelliffe, 1913). It is seen in the absence of paralysis, muscle palsies, and sensibility disturbances, and is characterized by a loss of ability to carry out rapidly alternating movements, such as flexion and extension of the forearm on the arm. In dogs, birds, rats, and other animals poisoned by nitrobenzene, it was observed that at times one set of muscles would be contracted and another set relaxed, and at other times just the reverse happened. For example, if motor impulses passed to the extensors of the hind legs, the animal was unable to stop these impulses or to use the antagonistic muscles, and the leg remained for a time rigidly extended; again, if the impulses passed to the flexors, then the animal was unable to extend the leg. This condition, according to Babinski, indicates involvement of the cerebellar paths.

*Nystagmus.*— According to Jelliffe (1913), Holmes states that "nystagmus is a common and very valuable localizing sign of local cerebellar lesions. It is almost certainly a true cerebellar symptom." Nystagmus does not always appear, but when present it is invariably a cerebellar type, distinguishable from vestibular nystagmus by the jerky movements of the eyeball. The shifting is in a lateral plane, and is equally rapid in either direction.

*Asthenia.*— Asthenia is one of the first symptoms to appear and is almost invariably present. The animal is usually so weak that when it is placed on its feet, its legs literally double up beneath it, and its head sways about as if the neck were disjointed. This symptom, according to Jelliffe (1913), indicates "disorder of the tractus cerebellovestibularis spinalis, or rubro-spinalis."

*Hypotonus.*— Hypotonus, as revealed by palpation of the muscles and by special tests of the tendon reflexes, was observed in the more advanced cases, especially, of nitrobenzene poisoning. In some cases this symptom was accompanied by poor tendon reflex reactions, while in other cases the tendon reflexes were normal or even exaggerated. These conditions indicate cerebellar hypotonus.

*Disturbance of respiration.*— In moribund animals poisoned by nitrobenzene, one almost invariably observes a disturbance of respiration, and in some instances a slowing of the pulse rate. Musser (1904) states that cerebellar tumors often cause symptoms of this type.

*Headache and tenderness of the occiput.*— Headache in animals is very difficult, if not entirely impossible, to determine. However, certain actions exhibited by animals poisoned by nitrobenzene might be interpreted to indicate headache; for instance, the animal's desire to press its head against some object. Dog I was observed to stand for long intervals with its head pressed against the attendant's legs or against some solid object (page 431). And certainly the fact that the animal exhibited some discomfort if the back of its head was touched, indicated a tenderness in the vicinity of the occiput. These symptoms have been observed in cases of cerebellar tumors.

*Circus movements.*— Rotation of the head and the neck was always observed in the case of birds poisoned by nitrobenzene. This is a characteristic symptom observed in cerebellar pigeons. Rotation of the body about its longitudinal axis, observed especially in gray rats and sometimes in dogs, is a symptom exhibited in cerebellar mammals.

## CAUSE OF THE LATENT PERIOD

The fact that there often exists a long latent period, the period of time elapsing between the administration of the drug and the onset of the symptoms, has led to much theorizing as to its cause. The following two theories have been the most popular: the theory advanced by Ollivier and Bergeron and held to by Letheby, that nitrobenzene is converted into anilin in the body and that time is required for this transformation; and the theory investigated first by Filehne and accepted by most recent writers, that the drug is so lightly soluble in the tissues of the body that time is required for the absorption of it in sufficient amounts to produce the poisonous effects.

Filehne has ably shown that the action of the drug does not depend on its conversion into other chemicals. Furthermore, he failed to find any trace of anilin in any of the organs of animals poisoned by nitrobenzene even by the hypochlorite test. His criticism of the isophenylcyanide test (used by Letheby) is justified, since in conducting this test nitrobenzene

is itself converted into anilin. Filehne has shown also that the theory of slow absorption does not account for the rapid action of the drug observed in certain cases.

In all probability the rate of absorption of nitrobenzene by the body tissues does have something to do with the cause of the latent period; but the explanation must be primarily based on the readiness with which the drug is absorbed by certain tissues as compared with other tissues, and not alone on the rate of absorption by the tissues in general. It will be recalled that nitrobenzene is readily soluble in oils and the liquid fats; it is soluble also to a certain extent in lipoids, but probably to a less extent in certain lipoids than in others, and even the same lipoid may absorb the drug more readily under certain conditions than under other conditions.

When the drug is administered by vapor inhalation, the amount absorbed by the blood (at a given vapor pressure) depends, undoubtedly, on the amount and the condition of the fats or the lipoids in the blood. Also, the amount absorbed from the blood and held in solution by the body fats is, in all probability, directly proportional to the absorption power of the body fats over the absorption power of the fats in the blood.

Since nitrobenzene is more readily absorbed by the liquid body-fats than by the lipoids (of the brain), large amounts of it may be stored in the liquid fats of the body without the animal's showing any immediate symptoms of poisoning. Moreover, since the action of the drug on the cells of the brain probably depends on its concentration in the vicinity of these cells — as in the case of chloroform, ether, and other drugs that act directly on the cells of the brain — nitrobenzene, depending on the amount and the condition of the lipoids and the fats held in suspension in the blood, may be picked up from the body fats by the blood in such small amounts as to be in time entirely eliminated from the body without ever giving a sufficient concentration in the vicinity of Purkinje's cells to cause symptoms of poisoning; so that large amounts of the drug may be stored in the body without the animal's ever showing any symptom of poisoning.

On the other hand, depending on the concentration of nitrobenzene in the blood supply to the cerebellum, a sufficient concentration of the drug in the vicinity of the Purkinje cells might be reached, even after minute

doses, to affect these cells and produce the typical symptoms of poisoning, or even death, within a very short time after the administering of the poison.

If the above assumptions are correct — and they can be so proved only after a long series of experiments dealing more exhaustively with the physics, chemistry, and physiology of the subject — then it is not surprising that, as was found, the latent period, as well as the intensity of the action of the drug, should vary in different individual animals, or even in the same individual at different periods of time; for neither the amount nor the kind of fats in the blood or the nervous tissues is absolutely constant.

## CONCLUSIONS

The present work has confirmed the findings of previous investigators regarding all six of the points listed in the first paragraph following the review of the literature. In addition the following conclusions have been deduced:

1. Aside from the possible disturbance of digestive functions and a possible asphyxia due to a direct action of nitrobenzene on the blood, most, if not all, of the observed symptoms of nitrobenzene poisoning may be explained on the basis of disturbances in the cerebellum or the cerebellar paths.

2. Toxic doses of nitrobenzene, when administered by vapor inhalation, exert a direct action on the Purkinje cells in the cerebellum, causing chromatolytic degeneration of these cells.

3. Histological examinations have failed to reveal any definite changes in any of the organs of the body except the blood (presence of methemoglobin and morphological alterations of erythrocytes) and the cerebellum (chromatolytic degeneration of the Purkinje cells).[13]

4. The size of the lethal dose probably depends on conditions such as the amount and the kind of fats in the blood, which favor or disfavor a concentration of the drug in the vicinity of the nerve cells.

5. The latent period (the time elapsing between the administration of the poison and the onset of the symptoms) is undoubtedly due to the

[13] The writer does not mean to assert that histological changes do not occur in other tissues, especially in other parts of the central nervous system. Indeed, a further study of the present sections may yet reveal such changes. It would be strange if the action of nitrobenzene on the central nervous system were confined to a single type of cells only. Probably in cases of fatal poisoning other nerve cells are involved also, but it will be difficult to determine whether such changes are due to a direct action of the poison or are the result of a complication of changes attending death by poisoning. Further investigations are being made along this line.

absorption of the nitrobenzene from the blood, and its retention by the liquid fats of the body in which it is easily soluble. As the concentration of the poison in the blood lipoids and fats diminishes, in relation to its concentration in the body fats, the nitrobenzene is given up again to the blood; and in the course of time, a sufficient concentration of the poison in the lipoids of the cerebellar or other brain cells is reached to produce an onset of the motor symptoms. The time required to bring this about (the latent period) depends on the same factors as those on which the size of the lethal dose depends, and is undoubtedly hastened by the ingestion of solvents of nitrobenzene, such as alcohols, fats, oils, milk, and the like. Possibly, also, the condition of the brain lipoids at a given time may be an important factor in hastening or retarding the absorption of nitrobenzene by these lipoids.

6. Nitrobenzene cannot be used, with any degree of safety, for the fumigation of animals to destroy their external parasites. The lethal dose for birds and mammals is rather variable but it may be very small; and from these experiments it will be seen that apparently a shorter period of fumigation at a given temperature is required in order to kill a domestic animal than to kill even a fair proportion of either fleas or biting lice. However, as has been pointed out by the writer in a previous paper (Chandler, 1917), the drug may be used, with the exercise of caution, for collecting external parasites from animals, by fumigating the animals at low temperatures and for short periods of time — at a temperature not over 20° C., and for a period not longer than one and one-half hours. Under these conditions the parasites may be stupefied without any appreciable damage being done to the host; but the drug is dangerous to handle under any conditions.

7. Because of the extreme toxic properties and the subtle action of nitrobenzene, the following uses of this drug should be prohibited by legislation: for perfuming soaps, lotions, and pomades; as a solvent in shoe polish, floor wax, and the like; and especially as an ingredient of flavoring extracts, confections, and liqueurs. The drug should be regarded as one of the most dangerous of poisons, and its sale and use should be regulated by law just as in the case of any other deadly poison.

8. Nitrobenzene should be given serious consideration as an industrial poison. Munition plants, dye works, and other factories which handle

nitrobenzene, should be inspected with the view of installing devices to prevent workmen from inhaling the vapor or coming into contact with the liquid.

9. In view of the evident relation existing between the lethal dose of nitrobenzene and the amount and kind of fats and other solvents of the drug present in the blood, it would appear highly desirable that further investigations should be undertaken with the view of working out rational therapeutics for cases of poisoning.

10. Since the findings in these experiments indicate that the symptoms of nitrobenzene poisoning are caused by a direct action of the drug on the Purkinje cells, causing these cells to degenerate, and since different sets of muscles appear to be involved at different times, it would appear that further investigations might be of value from the standpoint of obtaining more exact data regarding the localization of functions in the cerebellum.

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# STUDIES IN THE REVERSIBILITY OF THE COLLOIDAL CONDITION OF SOILS

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# STUDIES IN THE REVERSIBILITY OF THE COLLOIDAL CONDITION OF SOILS

# STUDIES IN THE REVERSIBILITY OF THE COLLOIDAL CONDITION OF SOILS

A. B. Beaumont

The early workers in the field of colloid chemistry considered substances possessing colloidal properties to be distinct chemical individuals. Those working with soil problems spoke of certain inorganic and organic colloids. The colloids found, and thought to exist, in the soil were few in number. Colloidal silica, alumina, and ferric oxide among the inorganic compounds, and the various organic substances commonly designated as humus, are the most frequently mentioned in the literature. Additions have been made to this list from time to time, and occasionally sharp controversies have arisen as to whether the substance in question exists in the soil as a crystalloid or as a colloid. The contradictory results in many cases probably can be accounted for by the different geological conditions under which the soils studied have been formed.

The modern conception, as expressed by leading writers on the subject, is that colloids are to be considered as a state or condition of matter, not as chemical individuals. It has, of course, been long recognized that some few substances — for example, silica — exist both as crystalloids and as colloids. But recent investigations of Von Weimarn and others have so increased the number of substances that have been prepared in the colloidal conditions, as to lead some to believe that nearly all substances can exist as colloids as well as crystalloids; and Von Weimarn (quoted by Ostwald, 1915 : 101) has gone so far as to proclaim that "the colloid, like the crystalloid, is a universally possible state of matter."

It was in accordance with this modern conception of colloidality that the work herein described was undertaken, and the data presented show that the colloidal condition of the soils worked with is dependent, in a degree at least, upon circumstances and environment. The object of the work undertaken was to throw some light on the physical changes, and their effects, which a soil undergoes with variations in its moisture content, especially on being wetted and dried. As is shown later, the prob-

lem has been attacked in many ways previously. It was thought well to attack it from the standpoint and with the methods of colloid chemistry. It has resolved itself into a study of the reversibility of the colloidal condition of soils.

## REVERSIBILITY DEFINED

Several different meanings have been attached to the word *reversibility*. According to Ostwald (1915 : 40), "when a change in the state of a colloid may be reversed by reversing the conditions which brought that change about, it is said to be 'reversible.'" The word is commonly applied to the change between the sol and gel conditions. Thus, if a colloid which has been precipitated by a salt goes back into solution on removal of the salt by washing, the colloid change is said to be reversible; if this does not occur, the colloid change is irreversible.

Ostwald states that the reversibility of a change is not determined, in the main, by the nature of the colloid itself, but by the character of the conditions that produce the coagulation. For instance, the precipitation of the typical protein sols by neutral salts is reversible, whereas their precipitation by heat is irreversible. Ostwald states that one cannot, therefore, properly speak of reversible and irreversible colloids, but only of reversible and irreversible changes.

Zsigmondy (Zsigmondy and Spear, 1917) divides colloids into reversible and irreversible, depending on whether or not they leave a soluble residue on evaporation. The irreversible colloids he still further divides into two groups: to the first class belong those that coagulate in dilute solution and precipitate in the form of a powder rather than as jelly; the second class consists of those that may be considerably concentrated before coagulation sets in, and whose precipitates are decidedly jelly-like, such as colloidal silicic acid, clay, and ferric oxide. The colloids of the first group are considered completely irreversible. Those of the second group, which includes some most commonly found in the soil, can, on the other hand, be brought back to the hydrosol state by the addition of a small quantity of a suitable reagent, provided the residue has not been too thoroly dehydrated.

Typical reversible colloids, after sufficient swelling has occurred, dissolve in a solvent to give a homogeneous-appearing solution. Gum arabic, albumin, and ordinary glue are good examples.

The meaning of the word *reversibility* as above interpreted is too narrow when applied to soils. Ehrenberg (1915) states that the meaning is not so much erroneous as of too little extension. In dealing with soils from the agricultural standpoint the cases in which a hydrosol is possible are the exception, not the rule. Such cases would be the flooding of rice fields, cranberry bogs, and other soils the crops or the culture of which require an excess of water at times. Reversibility of soil colloids in the narrow sense above described would be of more or less importance in the case of a temporary excess of water, as in rains and in the application of irrigation waters, especially by the flooding methods. From the standpoint of the geological formation of alluvial, lacustrine, and marine soils, this sort of reversibility would be of considerable importance.

However, in considering the reversibility of the colloidal state of the great masses of agricultural soils, one's concern is more with the change from the gel to the non-gel form and vice versa. The reversibility studies of Van Bemmelen with various oxides dealt with the gel and non-gel forms, and the word *reversibility* is used by some writers in referring to those changes. It is a word which is convenient to use and is expressive.

In a consideration of the reversibility of the colloidal condition of soils, it seems that the indirect cases which occur thru chemical and biological actions should be included, such as the hydration of iron salts, the action of bacteria, and the growth of lower forms of plant life. It will be seen in the presentation of results that some of these actions are considerably affected by changes in the moisture content of the soil. Reversibility of the colloidal state of soils should include, therefore, all cases brought about by physical, chemical, and biological agencies or a combination of these. In fact, most of the changes of the colloidal states of soils are probably due to a combination of forces. These changes may be represented as follows:

$$\text{Non-colloidal state} \rightleftharpoons \text{Colloidal state} \begin{cases} \text{Sol} \\ \uparrow\downarrow \\ \text{Gel} \end{cases}$$

## COLLOIDAL MATERIALS IN SOILS

Way (1854) reported deposits of soluble or gelatinous silica in the lower beds of the chalk formation. The silica, soluble in alkalies, in the samples examined ranged from 5 to 72 per cent.

Schloesing (1874) was one of the first to call attention to the colloidal matter of soils. From a clay he isolated a gelatinous mass which consisted mainly of water, silica, and alumina, with small quantities of ferric oxide, magnesia, and potassa.

Van Bemmelen (1888) attributed the absorptive properties of soils largely to the colloidal matter which he believed to surround most particles of soils. This matter consists of ferric oxide, silica, silicates, and organic matter in various stages of decomposition. These materials unite with one another or with other substances to form what Van Bemmelen designated as *adsorption compounds*.

Warington (1900) claimed that true colloidal clay is always an aluminum silicate, but also mentioned the presence in some soils of ferric oxide, hydrated alumina, and colloidal humus.

Schloesing (1901) states that colloidal alumina occurs in European soils in very small quantities, but he found very much free alumina in soil samples from Madagascar. This results from the weathering of silicates and later hydrolysis, as in the case of colloidal ferric oxide. Hilgard (1911) inclines to a similar view, and sees in the presence of gibbsite and bauxite a reason for the assumption of the free alumina in soils.

Cameron and Bell (1905) dispute the presence of colloidal alumina in normal soils. Lacroix (1914) reports it in the decomposition products of aluminum silicates, and McGeorge (1916) reports having found it in the soils of Hawaii.

Ries (1908) includes among the ingredients of clay that may assume a colloidal form, aluminum hydroxide, iron hydroxide, hydrated silicic acid, and organic matter.

Hilgard (1911) considers that colloidal clay is clay which will remain suspended in a column of water eight inches high during twenty-four hours, and that the nature of this colloidal clay varies considerably in composition. According to this author, colloidal clay contains ferric hydrate and other colloidal, or at least amorphous, substances such as silicic, aluminic, and zeolitic hydrates.

Gans (1913) and Wiegner (1912) carried on an extended controversy as to whether an artificially prepared colloidal silicate was a chemical compound or a mixture of gels. Wiegner was of the opinion that it was a mixture of gels, and that owing to its similarity to the natural soil zeolites

they also are mixtures of colloidal gels. Gans thought that the substance was a chemical compound, but admitted the possibility of its existing in the colloidal state.

Ehrenberg (1915) classifies soil colloids broadly into systems based on the physical condition of their phases. Colloidal silica and humus are placed in the liquid-liquid system, and the colloidal ferric oxide and alumina in the solid-liquid system.

Colloidal silica originates from the remains of plants and from the weathering of rocks. The final state may be colloidal or crystalloidal, depending on the speed of the reaction. If the change is rapid, a colloid such as opal may be formed; while if it is slow, quartz crystals are formed.

Iron compounds occur in soils in relatively large quantities and widely distributed. If these become dissolved in water, colloidal ferric oxide easily forms by hydrolysis under ordinary conditions. With difficultly soluble iron compounds such as silicates, weathering and consequent solution are necessary.

Microscopic plant and animal life are colloidal. Altho bacteria may be present in large numbers, because of their comparatively small mass they are not very important as compared with other soil colloids.

Colloidal humus originates from all sorts of plant and animal remains, is not chemically defined, and varies in all degrees between solid and liquid. It stands on the boundary line between a colloidal and a crystalloidal condition, as shown by a slight dialyzability and conductivity.

Spear (Zsigmondy and Spear, 1917) states that colloidal silica, silicates, hydroxides of iron, aluminum, and manganese, and colloidal matter such as humus, exist in the soil.

From what has been said so far it is evident that a great many materials existing in the soil in the colloidal condition have been identified and studied. There is little doubt (Ehrenberg, 1915) that many other substances exist in the soil in this condition, and that, as methods of colloid chemistry are further developed and the range of soils examined is extended, additions will be made to the list. It is possible that every soil constituent will be found to exist in the colloidal condition under some circumstances.

Methods for determining the amounts of colloids in soils have not been sufficiently developed to enable one to determine these amounts with any great degree of accuracy. At best, the measurement is only an estimation. Evidence of the unsatisfactory status of methods exists in the

great number that have been evolved from time to time and used with varying success by different investigators.

There is little doubt that the amounts of colloids in soils vary considerably with the kind of soil and the conditions. Schloesing (quoted by Ehrenberg, 1915) estimated that the colloidal clay of normal agricultural soils seldom exceeds 1.5 per cent. However, he found as much as 35 per cent of colloidal matter in extremely heavy soils.

Hilgard (1911) estimated the amounts of colloidal clay in soils as varying from 0.5 per cent for very sandy soils to 45 per cent and over for heavy clay soils.

Tempany (1917) calculated the amounts of colloidal matter in soil from their linear shrinkage on drying, and gives figures varying from 9 to 64 per cent.

## REVIEW OF LITERATURE

It has been observed by many investigators that for some soils previous drying is beneficial from the standpoint of plant production. This benefi has been ascribed by some writers to the effect on the physical condition of the soil. Alternate wetting and drying has been considered particularly efficacious in this respect. Of late the effect on the colloidal matter in particular has become a favorite assumption of some writers. In other cases the benefits of drying or of alternate drying and wetting are attributed to chemical or biological effects, or to a combination of these with physical effects. On this point Lyon, Fippin, and Buckman (1915:188) say: "Just what may be the effects of wetting and drying on the colloidal matter of soil is a question."

The increased productiveness of soils due to fallowing is also a matter of common experience. The stirring of the soil is accompanied by rapid drying. To what extent the benefits are due to physical, chemical, or biological effects, has not been worked out.

Buckman (1911) concluded from the work of others that under conditions of extreme dryness an increase in moisture means an increase in nitrates. Lyon and Bizzell (1913) found that an increase in moisture after a dry period was sometimes accompanied by an increase in nitrate in an unplanted soil, and Lyon (1907) expressed the opinion that a dry period previous to the time of heading causes wheat to be harder and higher in protein.

The beneficial effects on fertility from burning the soil have long been known. In Europe and England the practice of burning, and of paring and burning, the soils was very common at one time. It has been thought by many that the beneficial effects of this practice were due to a physical bettering of the soil (King, 1906).

It has been observed in India (Howard and Howard, 1910) that the drying of the alluvial soils in direct sunlight increases their productivity, and some of the natives make a practice of exposing their soils to this ameliorating influence.

According to Alway and Vail (1909), the moistening and drying-out of soils under some conditions causes a natural fertilization of the deeper layers due to the falling of the organic matter into the cracks.

Ehrenberg (1915) states that many investigators have observed a bettering of the quality of the soil as a result of its drying out, and quotes Vanha as saying that the energetic drying-out of soils rich in humus favors the quality of such soils especially.

In connection with the benefits of drying soils, Ehrenberg cites the old custom of using garden walls made of loam as a fertilizer; and King (1911) tells of the practice among the Chinese of tearing out "kangs" that have been made of clay subsoil and thoroly dried, and using them as fertilizer.

Ehrenberg is of the opinion that only soils containing considerable organic matter are affected by drying. The effects of drying upon other soils are very slight indeed, and are quickly lost on the soil's being wetted, according to that author.

The effects of drying the soil are sometimes injurious. Hilgard (1911) reports injuries to plants caused by the drying and cracking of soils and the consequent mechanical tearing of the root systems. Sometimes the shrinking of the surface crust of soil around the stems of grain causes a constriction that is injurious. Ehrenberg has reported that a disease of sugar beets is traceable to such mechanical injury.

Mathews (1916) has pointed out the importance of moisture conditions in the irrigation of certain heavy soils. If the surface of these soils has been dried and then wetted, the irrigation water enters slowly, due to the swelling of the soil and the closing of the cracks.

The extensive literature bearing on the specific physical, chemical, and biological effects of moisture changes in soils has been rather fully sum-

marized by Cameron and Gallagher (1908), Lyon and Bizzell (1910) Kelley and McGeorge (1913), and Klein (1915).

Cameron and Gallagher show a variation in the volume of soils with repeated wetting and drying, depending on the previous condition of the soil. Finally a condition of natural packing is reached, at which the expansion on wetting is equal to the contraction on drying.

Lyon and Bizzell found, along with other investigators, that the effect of steam sterilization was to increase the soluble matter of both organic and inorganic constituents. This increase was particularly marked in the case of organic matter.

Kelley and McGeorge studied the water and acid extracts of different soils that had been air-dried and others that had been dried at higher temperatures. They found that on an average the solubility of the constituents increased with the temperature of drying. Iron was an exception. The high solubility of the soils used in aquatic agriculture is according to these investigators, decreased by drying. They say the subject is very complex, and among the many factors involved are floccu lation of colloids, oxidation, deoxidation, decomposition, dehydration, and the attending physical alterations of the soil film.

Klein's work is divided into two parts. In experiment 1, the effect o partial drying of soils on total water-soluble salts, nitrates, potassium calcium, and acid-soluble phosphorus, and on the growth of plants, is studied. In experiment 2, the effect of complete air-drying on the pro duction of carbon dioxide and nitrates is studied. In this experiment the soils were repeatedly wetted and dried, three dryings being the maximum Klein arrived at the following conclusions, among others:

In experiment 1: (1) Drying the soil previous to planting has a bene ficial effect on plant growth. (2) The water-soluble matter is increased by drying in a soil low in organic matter, but is decreased in a soil high in organic matter. (3) Drying the soil has but little effect on the avail able potassium, calcium, and phosphorus of the soil.

In experiment 2: (1) Bacterial activity, as measured by carbon-dioxid production, is increased by a previous drying of the soil. (2) Previou drying increases the soil nitrification, reaching a maximum with three dryings. The author thinks that the physical effects of drying are important in this connection, and that the flocculation of the colloida material is very important.

Christensen (1917) states as a result of his studies that the ability of soils to free acid from calcium-acetate solution is from two to four times as great in the air-dry as in the moist condition, a result just the opposite of what was expected. With litmus solution and litmus paper, however, practically no difference was noticeable as a result of drying.

The classical and fundamental researches of Van Bemmelen (1909) on the reversibility of the hydrogels of various oxides have supplied the greater part of the knowledge on this subject. He worked particularly with the hydrogel of silica. By placing the hydrogel in desiccators, each with a different vapor pressure, he obtained data which showed that the final dehydration depends on the preparation and previous history of the gel and on the vapor pressure at a given temperature. It was found that by lowering and raising the vapor pressure, within certain limits, dehydration and rehydration are possible repeatedly, altho the reversibility is not always along the same path or complete. In other words, unless dehydrated too far the dried gel eagerly took up water again, but did not take up as much as it previously had nor did the volume return to its original size.

According to Cushman (1904), if the hydrogel of silica is heated to a temperature of about 1000° C. it loses its power to take up moisture to any great extent. However, a small amount of moisture is taken up.

Van Bemmelen worked also with colloidal oxides of alumina, iron, and other metals. For ferric oxide and alumina he found results similar to those for silica but with minor differences in regard to transition points.

Zsigmondy (Zsigmondy and Spear, 1917) points out that irreversible colloids may become reversible by the addition of reversible colloids. This is probably an adsorption phenomenon, and opens up interesting possibilities because of the lack of uniformity in the composition of soils.

Muller (1907) prepared a reversible colloidal alumina by peptizing a freshly precipitated aluminum hydroxide with hydrochloric acid. The hydrosol thus obtained is fairly stable, and leaves a precipitate which is soluble in water.

Ehrenberg (1915) reports Schloesing as saying that an artificial clay may be made by mixing 1 per cent of glue with finely pulverized sand. This mixture exhibits reversibility of properties, cohesion, and plasticity, on being dried and wetted.

Hilgard (1911) observed that his "colloidal clay," which could be obtained from a suspension either by evaporation or by flocculation, exhibited reversibility. When it dried it shrank as so much boiled starch, and on being remoistened it swelled quickly, resuming its former jelly-like consistency. Moistened with less water it became highly plastic and adhesive.

Grout (1906), in attempting to raise the plasticity of clays, found that agar-agar mixed with clay was effective but alumina cream was less effective. Furthermore, after being air-dried, powdered, and mixed, the plasticity of the alumina cream as used was irreversible. Grout also prepared an artificial hydrated silicate of alumina, and found that this also was irreversible after drying.

Ashley (1909), in commenting on Grout's work, said it seemed to Grout that none of these or other colloids could be responsible for the behavior of natural clays; for he apparently thought that clay could be dried and wetted repeatedly without injuriously affecting its plasticity, or, in other words, without affecting the activity of the colloids. Ashley said further that in this supposition Grout was not in accord with practical experience. Clay used by potters has in most cases never been deprived of its natural moisture. After once being dried out at as low a temperature as 60° C., it is found to have lost noticeably in plasticity.

Ehrenberg (1915) cites the work of Thaer and Ostwald, and states that it can be said with a considerable degree of certainty that humus is reversible. How far humus is affected by aging is not known. The study of it is restricted by its not having a definite chemical composition.

Little is known concerning the behavior of humus gel, according to Ehrenberg, but he states that according to Zailer and Wilk humus gel does not suffer many changes in drying out; that it exhibits simple swelling phenomena, but does not come back to its original volume if it is more or less dried. To substantiate this point he cites data from Wollny showing that the greater the depth at which dried peat was taken, the more it increased in volume on being moistened. The surface layers, having been dried the more, increased less.

Warington (1900) cites Schloesing's experiment in which he mixed calcium humate with clay and found that the humate had considerable cementing power, which it lost on being dried. The irreversible character here is probably due to the absorption of the calcium in the preparation

of the humate. Humus gel made by evaporating the sol, as ordinarily prepared, is reversible.

Rohland (1914) reports that the adsorptive power of soil colloids for water decreases after repeated drying, but that new colloids are formed by clays standing in an excess of water.

According to Ehrenberg (1915), Schubler reported that a humus colloid prepared by him could not take up as much water after drying out as before. Wiegmann confirmed this statement. A similar observation was made by Schubler on a strongly humus-containing soil. Lasius reported that peat once dried does not soften again, and Ruhlmann stated that peat when once air-dried cannot be brought back to its original slimy condition thru working.

Tacke and Immendorff (1898) report that peaty soils not only shrink strongly by natural or artificial drying, but that they lose their swelling capacity, take on a peculiar sandy condition, and never again become strongly colloidal. Further, these investigators report that the solubility of phosphoric acid in moor soil is increased by drying the soil at about 80° C. They also found an increase in the water-soluble potassium and calcium, due to drying out. This effect was masked by using 0.5-per-cent hydrochloric acid as a solvent.

Mitscherlich (1902), working with moor soil, found that moistening and then drying at 100° C. affects the soil structure so that it holds less water. He concludes that moistening and drying a soil is not a simple reversible process.

The destruction of the crumb structure of soil in good tilth by the beating of rains has been recorded by several writers, including Warington, Hilgard, and Ehrenberg. This is a case of deflocculation brought about by physical agencies.

Harrison (1917) reports that wet methods of cultivation when first applied to paddy soils tend to bring about a physical deflocculation followed by a weathering of particles, thus causing the soils to become heavier. This heaviness is probably due to a production of the colloidal condition.

Tempany (1917), in studying the shrinkage of the soils of the West Indies, assumes that the gel condition of the colloidal matter in these soils is restored by moistening and kneading the air-dry soil — a case of physical reversibility, largely.

In ceramics the practice of increasing or bringing back the plasticity of clays by keeping them soaked with water for several months is a common one. The effect of this aging as well as weathering may be the production of the colloidal condition by hydrolysis, according to Ries (1908). Mechanical grinding is often as efficacious as aging in improving plasticity. In this connection Rohland (1911) says: "By repeated moistening with water the amount of colloids is increased and thereby plasticity is raised."

Ruprecht and Morse (1917) show the positive presence of soluble salts of iron, aluminum, and manganese in soils long treated with ammonium sulfate, and it is to these soluble salts that toxicity is ascribed. Morse and Curry (1908) show that the presence of calcium carbonate prevents the formation of soluble iron and aluminum salts in soils treated with certain solutions.

The soil from limed plats shows a greater adsorption for dyes than does that from unlimed plats (Ruprecht and Morse, 1915). This indicates more colloidal matter due to the liming. As pointed out by Ruprecht and Morse, this is probably due to a flocculation or a precipitation of the iron and aluminum in some form by the calcium compounds. If so, this presents a case of chemical reversibility which is of importance as regards the toxic effect of ammonium sulfate long used as fertilizer.

In the formation of iron-pan in moor soils, as cited by Warington (1900), a similar case of chemical reversibility of the colloidal condition is presented. The iron passes into the soil as soluble salts and is later precipitated as colloidal ferric oxide. Under certain conditions this may again go into solution and the process be repeated.

## *Summary of literature cited*

While the observations and the results of investigations that have been mentioned are more or less conflicting, it seems that the following points stand out:

1. Previous drying of a soil is, in general, favorable to its fertility.
2. Data have been obtained which show that this effect on fertility may be traced to physical, chemical, and biological causes.
3. Drying and wetting some soils produces volume changes, and affects the water-holding capacity, the penetrability, and other physical properties.

4. Alternate drying and wetting of some soils favors some of the soil activities which are correlated with fertility.

5. Previous drying increases the solubility of inorganic and organic constituents, such increase usually accompanying an increase in the temperature of drying.

6. Soils containing considerable organic matter are affected by moisture changes to a greater degree than are those containing small amounts of organic matter.

7. Changes in certain physical properties of soils, such as cohesion and plasticity, are, to a degree at least, reversed by moisture changes.

8. Changes in the properties of soils due to moisture changes have been attributed by many workers to changes in the colloidal condition.

9. Studies with more or less pure colloidal materials usually found in the soil in the colloidal condition indicate a possible reversibility of all these materials under some conditions.

10. Most of these studies cited have been on soil properties other than colloidal, and with methods other than those of colloid chemistry.

## EXPERIMENTAL WORK

### *Study of methods*

Snyder (1917) lists eighteen possible methods, under eight distinct headings, for measuring the colloidal content of soils. The relative merits of some of these have been discussed fully by Stremme and Aarnio (1911), and Snyder reviews all of them.

Altho most writers on the subject are of the opinion that the method of water-vapor adsorption, originally devised by Mitscherlich (1905), is the best general method for measuring colloidal content, Snyder thinks that the dye-adsorption method, first used by Ashley (1909), has the greatest possibilities. Snyder recognizes the specificity of dyes for particular colloids. These two methods are undoubtedly the most feasible and practicable at present known.

Owing to the unsatisfactory status of methods for measuring colloidality, it was felt necessary to investigate some points most commonly disputed. Also, in the attempt to use various methods, some difficulties were encountered which required settling. Some time was spent, therefore, in preliminary work on methods before they were worked out as

finally used. As some of the data obtained may be of interest, they are here presented.

*Effect of temperature on adsorption of water vapor.*— The effect of temperature on adsorption of water vapor is a point that has been disputed. Patten and Gallagher (1908) and some other investigators (Taylor, 1915) have found a decrease in adsorption with an increase of temperature. This is what one would expect from a consideration of Le Chatelier's theorem, for adsorption is accompanied by a liberation of heat, a rise in temperature. Therefore, raising the temperature would tend to reduce adsorption rather than to increase it.

Hilgard (1911), Lipman and Sharp (1911), and recently Alway, Klein, and McDole (1917), on the other hand, think that the amount of water vapor adsorbed increases with the rise in temperature. The experimental work of hygroscopicity determinations has a high probable error. This should be taken into consideration in drawing conclusions from the data, which was not done by any of these investigators.

In order to learn whether any great differences were obtainable with slight variations in temperature, adsorptions were run at various temperatures. The results are given in table 1. The results show differences, but in no case is the difference sufficiently greater than its probable error [1]

TABLE 1. EFFECT OF TEMPERATURE CHANGES ON THE ADSORPTION OF WATER VAPOR BY DUNKIRK SURFACE SOIL

| | Per cent* of water vapor adsorbed | Difference |
|---|---|---|
| At 15° C. | 3.450±0.055 | |
| | | 0.175±0.066 |
| At 20° C. | 3.275±0.037 | |
| | | 0.095±0.066 |
| At 30° C. | 3.180±0.055 | |
| | | 0.150±0.097 |
| At 40° C. | 3.330±0.080 | |

* Unless otherwise stated, all percentage calculations in this article are based on oven-dried weights of soil.

[1] The probable error of the mean in this and all other experiments cited in this article was calculated by means of Peter's approximation formula, given by Mellor (1913). The probable error of the mean is $\frac{0.8453 \sum (+v)}{n\sqrt{(n-1)}}$, in which $\sum (+v)$ is the sum of the deviations of all the individuals from the mean, without regard to the sign, and $n$ is the number of individuals. If the difference between means is 3.8 times its probable error, the chance is 30 to 1 (Wood and Stratton, 1910) that the difference is significant.

to justify the drawing of the conclusion that temperature variations of from 5 to 10 degrees, within the limits of the experiment, make an appreciable difference in the amount of water vapor adsorbed.

These data, being limited, are not to be taken as conclusive as regards the question. It was thought justifiable, however, to disregard slight variations in temperature and to run all tests at room temperature. In order to reduce the fluctuations in temperature, the apparatus was put into a thick-walled, insulated, wooden box.

*Water-vapor-adsorption method not equally applicable to all soils.*— Originally it was intended to use in the experiments a glacial clay subsoil of the Dunkirk series. The sample used was taken from an excavation at a depth of about eight feet. The soil was placed in a humidifier, along with surface soil of the same series but from a different locality. In this particular experiment, saturated strips of heavy cardboard were used instead of the cotton cloth mentioned later in connection with other experiments. The results of this experiment are given in table 2. A gradual increase in the amount of water vapor adsorbed by the subsoil

TABLE 2. ADSORPTION OF WATER VAPOR BY A NORMAL (DUNKIRK SURFACE) AND AN ABNORMAL (GLACIAL SUBSOIL) SOIL

| Time exposed | Per cent of water vapor adsorbed by | | | |
|---|---|---|---|---|
| | Dunkirk surface soil | | Glacial subsoil | |
| | Dry | Moist | Dry | Moist |
| 7 days | 3.38 | 4.35 | 27.25 | 30.7 |
| 12 days | 3.50 | 4.27 | 38.90 | 40.6 |
| 17 days | 3.75 | 4.45 | 48.70 | 52.4 |
| 24 days | 3.47 | 4.23 | 57.00 | 61.2 |

may be noted, free water being present after seven days; whereas the surface soil showed no more variation in the amount adsorbed than could be ascribed to experimental error.

These results show a weakness in the water-vapor-adsorption method, namely, that some soils adsorb an abnormal amount of water vapor and therefore cannot be used in such experimentation.

The unusual adsorption appears to be due to the chemical rather than to the physical condition of the soil, and is therefore, properly speaking,

absorption. The subsoil was known to contain large quantities of soluble salts, among which were calcium magnesium and chlorine ions. As a consequence of this irregularity, this subsoil was eliminated from the tests of water-vapor adsorption.

*Effect of kind and source of dye on adsorption.*— In searching for a dye that would be adsorbed by colloidal ferric oxide, dyes from twenty-three sources were examined. The tests were made in both distilled water and approximately 0.1-per-cent ammonia water. Some of the dyes used are tabulated by various writers as acid dyes, and theoretically, therefore, would be adsorbed strongly by colloidal ferric oxide, which is basic. Only one, however, of all those examined was found to be adsorbed sufficiently strongly by colloidal ferric oxide to warrant its use. This was diamine sky-blue.

The effect of the small amount of ammonia on adsorption was very noticeable in some instances. In some cases it increased adsorption; in other cases it decreased adsorption; and in still others it changed the intensity or color of the dye. The effect of electrolytes on the adsorption of dyes was pointed out by Bancroft (1914), and should not be ignored in working with soils.

*Effect of the chemical composition of minerals on dye adsorption.*— During the experimentation on the adsorption of dyes by artificially prepared colloids, it was found that the chemical composition of the material had a great deal to do with the adsorption. For instance, methylene blue, a basic dye, is adsorbed strongly by colloidal silica but not at all by colloidal ferric oxide; whereas diamine sky-blue, an acid dye, acts in just the opposite way with respect to these two materials. In other words, according to this fact, neither dye is sufficient for measuring the total colloidal content of the soil, provided that approximately pure colloidal silica and ferric oxide are present.

In this connection it was thought advisable to ascertain whether the chemical composition of certain soil-forming minerals is an important factor in their adsorption of dyes. The minerals listed in table 3 were finely ground, and 1-gram samples were shaken with equal quantities of dyes. As far as it was possible to make them, the checks of the two dyes were of the same intensity.

TABLE 3. ADSORPTION OF METHYLENE BLUE (BASIC DYE) AND DIAMINE SKY-BLUE (ACID DYE) BY SOIL-FORMING MINERALS

(Relative intensities of solutions after adsorption shown)

| Mineral | Methylene blue | Diamine sky-blue |
|---|---|---|
| Ground quartz $SiO_2$ | 23.0±0.8 | 22.5±0.4 |
| Halloysite $H_4Al_2Si_2O_9 \cdot H_2O$ | 355.0±4.0 | 40.0±0.0 |
| Pyrophyllite $H_2Al_2(SiO_3)_4$ | 46.0±0.0 | 23.0±0.8 |
| Kaolinite $2SiO_2 \cdot Al_2O_3 \cdot 2H_2O$ | Clear | 120.0±4.3 |
| Prehnite $H_2Ca_2Al_2(SiO_4)_3$ | 27.5±0.4 | 26.5±0.4 |
| Natrolite $Na_2Al_2Si_3O_{10} \cdot 2H_2O$ | 26.5±0.4 | 25.0±0.0 |
| Siderite $FeCO_3$ | 24.0±0.8 | 34.0±0.0 |
| Hematite $Fe_2O_3$ | 34.0±0.0 | 29.0±0.8 |
| Limonite $2Fe_2O_3 \cdot 3H_2O$ | 23.0±0.8 | 75.0±0.0 |
| Calcium sulfate $CaSO_4$ | 22.0±0.0 | 38.0±0.8 |
| Calcium carbonate $CaCO_3$ | 22.0±1.7 | 45.0±0.8 |
| Calcium hydrate $Ca(OH)_2$ | *16.0±1.7 | Clear |
| Check | 25.0 | 25.0 |

* Purplish tinge. Difficult to read.

It can be seen that, in general, the adsorption of methylene blue is greater by the acid minerals. Kaolinite shows the greatest adsorption of this dye, and acts more like colloidal silica than does ground quartz, which adsorbs very little.

With diamine sky-blue the correlation between chemical composition and dye adsorption is less well marked. However, calcium hydrate, the most basic, is also the most adsorptive of this dye. In this case flocculation probably plays a part. Kaolinite adsorbs this dye more strongly than would be suspected from its composition. It is very likely that the great amount of internal surface of this mineral overrides any chemical effect on adsorption.

Rohland (1914) has pointed out that certain classes of dyes are adsorbed by certain kinds of soils.

*Effect of lower forms of plant life on dye adsorption.*— In the course of the experiment some results were obtained indicating that the plant life which had grown in the soil was affecting the adsorption of dyes. It was known that certain dyes are used by plant physiologists and bacteriologists in staining organisms. In order to get definite data on this point an experiment was run, using a fungus and an alga. That the possible effect of the soluble matter on the dye might be done away with,

a water extract of the material was used as a check. Results are given in table 4:

TABLE 4. ADSORPTION OF DYES BY LOWER FORMS OF PLANT LIFE

| Dye used | $(C-C_1)$·dye adsorbed by water extract | $(C-C_1)$·dye adsorbed by water extract plus fungus or alga | Difference |
|---|---|---|---|
| (a) A fungus (Botrytis) | | | |
| Methylene blue | 78.7±0.2 | 91.9±0.16 | 13.2±0.26 |
| Diamine sky-blue | 83.6±0.5 | 92.6±0.22 | 9.0±0.55 |
| Malachite green | 80.0±0.0 | 95.8±0.06 | 15.8±0.06 |
| (b) An alga (Cladophora) | | | |
| Methylene blue | 797.9±3.3 | 993.8±0.03 | 195.9±3.3 |
| Diamine sky-blue | 824.5±2.5 | 960.0±....* | 135.5±...* |
| Malachite green | 877.2±2.0 | 933.3±1.87 | 56.1±2.7 |

* No probable error. Cloudy. Difficult to read.

The differences are significant, and from them it is evident that both alga and fungus adsorb dye. The alga was found to be very adsorptive. Therefore, in dye-adsorption experiments where there is a chance for these organisms to grow, they should be taken into consideration.

The point just made is further substantiated by the data presented in table 5. The treatment of the soils was the same except for sterilization. They were allowed to remain moist for several months after sterilization and before the dye-adsorption experiment.

TABLE 5. EFFECT OF PREVIOUS STERILIZATION ON THE ADSORPTION OF METHYLENE BLUE BY DUNKIRK SURFACE SOIL

| | $(C-C_1)$·dye adsorbed | Difference |
|---|---|---|
| Sterilized, no growth apparent | 82.25±0.38 | 6.75±0.39 |
| Not sterilized, growth apparent | 89.00±0.03 | |

*Methods used in this work*

At the outset the writer was of the opinion that some of the colloidal states could best be measured by certain methods and other states by

other methods. For example, a colloid in the dry state can perhaps best be measured by an adsorption of water vapor, since the adsorption of a dye from solution would introduce the possible effect of free water on the condition. In the moist condition, on the other hand, the dye-adsorption method would not have that disadvantage at least. It was also thought wise to attack the problem with as many methods as were reasonably practicable. Results obtained during the course of the experimentation strengthened these opinions.

Three methods were used: (1) a slight modification of Mitscherlich's water-vapor-adsorption method; (2) a modification of Ashley's dye-adsorption method; and (3) the suspension method. The first and the second method were used the most extensively. The details of each method as finally worked out and used are as follows:

*The water-vapor-adsorption method.*— Five-gram portions of oven-dried soil or the equivalent were spread out as uniformly as possible in petri dishes having a diameter of approximately 10 centimeters. This gave in each dish a layer of soil with an average thickness of less than 1 millimeter.

The dishes with the soil were placed in desiccators containing a little 10-per-cent sulfuric acid in the lower part. By setting the dishes one on another, from five to seven dishes could easily be placed in the small desiccators and twice that number in the large desiccators. Mitscherlich used only one dish to a desiccator, which made the method exceedingly slow.

The dishes were separated from one another by mats of cotton cloth which had been saturated with the acid solution, the excess being removed by wringing. Each mat was kept from touching the soil in the dish below by means of a support made from a piece of cardboard and dipped into hot paraffin. The mats served to hasten the vaporization in the immediate vicinity of the soil. On the inner sides of the desiccators (humidifiers, properly speaking) were broad strips of cotton cloth, which were held in place by air pressure and adhesion and which dipped into the acid solution beneath. These served to bring up the liquid and hasten vaporization.

Hilgard (1911) used a wooden box, the sides of which were lined with blotting paper moistened with water to insure saturation of the air. Mitscherlich (1905) used 10-per-cent sulfuric acid in the bottom of the desiccator, but no strips of cloth or paper to hasten vaporization.

absorption. The subsoil was known to contain large quantities of soluble salts, among which were calcium magnesium and chlorine ions. As a consequence of this irregularity, this subsoil was eliminated from the tests of water-vapor adsorption.

*Effect of kind and source of dye on adsorption.*— In searching for a dye that would be adsorbed by colloidal ferric oxide, dyes from twenty-three sources were examined. The tests were made in both distilled water and approximately 0.1-per-cent ammonia water. Some of the dyes used are tabulated by various writers as acid dyes, and theoretically, therefore, would be adsorbed strongly by colloidal ferric oxide, which is basic. Only one, however, of all those examined was found to be adsorbed sufficiently strongly by colloidal ferric oxide to warrant its use. This was diamine sky-blue.

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| Natrolite $Na_2Al_2Si_3O_{10} \cdot 2H_2O$ | 26.5±0.4 | 25.0±0.0 |
| Siderite $FeCO_3$ | 24.0±0.8 | 34.0±0.0 |
| Hematite $Fe_2O_3$ | 34.0±0.0 | 29.0±0.8 |
| Limonite $2Fe_2O_3 \cdot 3H_2O$ | 23.0±0.8 | 75.0±0.0 |
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| Calcium hydrate $Ca(OH)_2$ | *16.0±1.7 | Clear |
| Check | 25.0 | 25.0 |

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It can be seen that, in general, the adsorption of methylene blue is greater by the acid minerals. Kaolinite shows the greatest adsorption of this dye, and acts more like colloidal silica than does ground quartz, which adsorbs very little.

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The treatments consisted of keeping moist, air-drying, and oven-drying (105° C.). The results of the experiment are given in table 6:

TABLE 6. ADSORPTION OF DYES BY ARTIFICIALLY PREPARED SOIL COLLOIDS

| | Time in contact | Moist | | Air-dried | | Oven-dried | |
|---|---|---|---|---|---|---|---|
| | | $(C-C_1)$ · dye | Difference | $(C-C_1)$ · dye | Difference | $(C-C_1)$ · dye | Difference |
| Silica and methylene blue | 1 day | 81.3±2.4 | 7.6±2.5 | 88.4±0.1 | 11.6±0.1 | 88.5±0.8 | 5.9±0.9 |
| | 8 days | 73.7±0.5 | 14.5±0.9 | 100.0 ... | Trace | 94.4±0.3 | 5.6±0.3 |
| | 15 days | 59.2±0.7 | | 100.0 ... | | 100.0 ... | |
| Humus and methylene blue | 1 day | 89.8±0.1 | 0.2±0.1 | 85.8±0.4 | 1.2±0.5 | 86.3±0.0 | 0.4±0.2 |
| | 8 days | 90.0±0.0 | 0.6±0.0 | 84.6±0.2 | 2.6±0.6 | 85.9±0.2 | 3.2±0.3 |
| | 15 days | 90.6±0.0 | | 87.2±0.6 | | 89.1±0.2 | |
| Ferric oxide and diamine sky-blue | 1 day | 100.0 ... | 0.0 ... | 82.0±0.1 | 2.2±0.5 | 83.2±0.4 | 4.5±0.7 |
| | 8 days | 100.0 ... | 0.0 ... | 84.2±0.5 | 0.9±0.7 | 87.7±0.6 | 2.8±0.8 |
| | 15 days | 100.0 ... | | 85.1±0.6 | | 90.5±0.6 | |
| Alumina and diamine sky-blue | 1 day | 100.0 ... | 0.0 ... | 79.9±0.1 | 2.9±0.8 | 80.4±0.3 | 2.9±0.3 |
| | 8 days | 100.0 ... | 0.0 ... | 82.8±0.7 | 0.7±0.8 | 83.3±0.0 | 0.7±0.5 |
| | 15 days | 100.0 ... | | 83.5±0.4 | | 84.0±0.5 | |

It is seen that in the moist material, with the possible exception of humus, maximum adsorption was reached in one day, and with silica there was a reversal of the adsorption process as the time elapsed. In both the air-dried and the oven-dried materials, with two exceptions, the amount of adsorption increased with the lapse of time. In most cases the differences are significant. They show that the condition of these colloids caused by drying is reversed by their standing in water, and that the reversal requires time.

Van Bemmelen (1909) has shown that the dried oxides of various metals will take up water vapor, and that there is a reversibility in this respect along some lines. The data in table 7 show the same thing for the commonest soil colloids, and also give a comparison of their relative adsorption of water vapor in three days:

TABLE 7. ADSORPTION OF WATER VAPOR BY AIR-DRIED, ARTIFICIALLY PREPARED, SOIL COLLOIDS

| Per cent of water vapor adsorbed by | | | |
|---|---|---|---|
| Ferric oxide | Alumina | Humus | Silica |
| 9.5±0.4 | 10.25±0.6 | 30.7±0.0 | 58.1±0.25 |

*Principal soils used*

Two surface soils and two subsoils were used in these experiments. These soils, consisting of Dunkirk surface soil, Clyde surface soil, Dunkirk subsoil, and Vergennes subsoil, represent a range of conditions. Their mechanical analyses, according to the centrifugal method of the United States Bureau of Soils, are given in table 8:

TABLE 8. MECHANICAL ANALYSES OF PRINCIPAL SOILS USED IN EXPERIMENTAL WORK

| | Dunkirk surface soil (per cent) | Clyde surface soil (per cent) | Dunkirk subsoil (per cent) | Vergennes subsoil (per cent) |
|---|---|---|---|---|
| Fine gravel | 0.170 | 0.145 | 0.000 | 0.020 |
| Coarse sand | 0.305 | 1.055 | 0.260 | 0.045 |
| Medium sand | 0.690 | 3.925 | 0.605 | 0.080 |
| Fine sand | 2.270 | 9.895 | 1.145 | 0.735 |
| Very fine sand | 9.590 | 11.525 | 12.145 | 1.595 |
| Silt | 74.030 | 53.330 | 65.800 | 22.960 |
| Clay | 12.945 | 20.125 | 20.045 | 74.565 |

The Dunkirk surface soil was obtained from Caldwell Field, Cornell University. According to the textural classification (Lyon, Fippin, and Buckman, 1915) of the United States Bureau of Soils, it is a silt loam. The sod was removed and the soil was taken from three to twelve inches below the surface.

The Clyde surface soil came from another field on the university farm, and represents a phase of the Dunkirk series which is rich in organic matter. These soils are naturally poorly drained and are much darker in color than the soils of the Dunkirk series proper. In getting the sample the sod was removed, as in the case of the Dunkirk surface soil. Texturally the Clyde soil is a silty clay loam.

The Dunkirk subsoil was taken at a depth of from one to two feet directly beneath the surface soil of the same series mentioned above. It is a silty clay loam texturally.

The Vergennes subsoil was obtained from Washington County, New York. Like the soils described above, it is a glacial lake soil, and, up to 1911 at least, it was the heaviest soil mapped by the United States Bureau of Soils. The sample was taken at a depth of from one to two feet. Texturally the soil is a clay.

The organic matter and the humus content of these soils are given in table 9. These were determined according to the official methods described in Bulletin 107 of the United States Bureau of Chemistry, with the exception that ammonium carbonate was used to flocculate the clay in the ammonia extract of humus as suggested by Rather (1911).

TABLE 9. ORGANIC MATTER (LOSS BY IGNITION) AND HUMUS OF PRINCIPAL SOILS USED IN EXPERIMENTAL WORK

| Soil | Organic matter (per cent) | Humus (per cent) |
|---|---|---|
| Dunkirk surface | 5.085 | 1.265 |
| Clyde surface | 14.540 | 4.340 |
| Dunkirk subsoil | 3.055 | 0.205 |
| Vergennes subsoil | 5.795 | 0.495 |

*Preparation of samples.*— After the soils were brought to the laboratory they were dried to a condition in which they could be worked readily without sticking, and then put thru a 2-millimeter sieve. Each lot of soil was then thoroly mixed before samples were selected for individual treatments. Certain lots were kept moist thruout the experimentation by placing them in air-tight jars; other lots were subjected to air-drying at room temperature and at 105° C.— the former being designated as *air-dried* and the latter as *oven-dried.*

The air-dried samples were usually dried by spreading the soil out in enameled pans in layers about $\frac{1}{4}$ inch deep. A layer of soil as thin as this usually dries very quickly. In case of alternate wetting and drying, the wetting was done with distilled water. No attempt was made to bring the soils to a definite moisture content; this was thought not worth

while, as such action does not occur in nature. The soils were saturated or a slight excess of water was added. The dried soils were usually lumpy, and before sampling they were crushed by means of a wooden rolling-pin.

*Effect of various factors on hygroscopicity*

It has been shown by Ehrenberg and Pick (1911) that dried soils adsorb less moisture than do moist soils, and these authors used this fact as an argument against Mitscherlich's method of determination of hygroscopic moisture. It is not known whether the difference is due to the effect of drying upon the colloidal material, or to the layer of adsorbed air on the soil (Ehrenberg, 1915).

*Effect of time.*— In order to learn whether this difference in hygroscopicity persists thruout a period of three months at least, an experiment was run to cover that point. The data are given in table 10:

TABLE 10. EFFECT OF TIME ON THE ADSORPTION OF WATER VAPOR BY CLYDE SURFACE SOIL

| Length of time in humidifier | Soil treatment | Per cent of water adsorbed | Difference | Ratio |
|---|---|---|---|---|
| 1 month | Air-dried | 12.15±0.30 | 3.80±0.48 | 1.31±0.045 |
| | Moist | 15.95±0.38 | | |
| 2 months | Air-dried | 12.20±0.25 | 4.80±0.49 | 1.39±0.04 |
| | Moist | 17.00±0.42 | | |
| 3 months | Air-dried | 12.70±0.10 | 4.05±0.32 | 1.32±0.03 |
| | Moist | 16.75±0.30 | | |

It is seen that the differences do persist as long as three months and that they are significant. Also, the ratios between the hygroscopicities at different periods are about constant. If the difference in hygroscopicity between moist and dry soil as shown by a test of one month is due to a failure to establish equilibrium, it seems that this failure still persists at the end of three months.

*Effect of remoistening.*— The second question to be studied was whether this drying produces a permanent effect on the hygroscopicity of the soil. Does remoistening restore the original condition? The data on this point are given in table 11. In order to preclude the possible effect of a failure to establish equilibrium, the remoistened soils were brought to a higher

moisture content than that of the continuously moist and undried soils with which they were compared. The comparison between any two conditions of the same soil were made in the humidifier at the same time.

TABLE 11. EFFECT OF REMOISTENING SOILS ON THEIR ADSORPTION OF WATER VAPOR

| Soil | Original water content (per cent) | Treatment | Per cent of water adsorbed | Difference |
|---|---|---|---|---|
| Dunkirk surface... | 10.7 | Continuously moist..... | 3.80±0.06 | 0.42±0.08 |
| | 25.0 | Air-dried and remoistened.. | 3.38±0.05 | |
| Clyde surface..... | 42.0 | Continuously moist..... | 18.9 ±0.2 | 3.1 ±0.04 |
| | 48.7 | Air-dried and remoistened.. | 15.8 ±0.3 | |
| Dunkirk subsoil... | 17.8 | Continuously moist..... | 5.77±0.01 | 0.51±0.02 |
| | 18.7 | Air-dried and remoistened.. | 5.26±0.02 | |
| Vergennes subsoil.. | 18.9 | Continuously moist..... | 17.60±0.05 | 0.20±0.07 |
| | 25.3 | Air-dried and remoistened.. | 17.40±0.05 | |

In every case the remoistened soils contained less hygroscopic moisture at the end of a week than did the continuously moist soils, altho the remoistened soils held more water at the beginning of the experiment. The differences, according to the standard set (footnote, page 492), are significant in all cases except that of the Vergennes soil, in which case the chances are 10 to 1 in favor of the continuously moist soil (Wood and Stratton, 1910).

These data indicate rather clearly that in the case of the air-dried soils the hygroscopicity is not immediately restored by remoistening. It may be observed that the greatest difference here is with the soil containing the greatest amount of organic matter and humus — the Clyde surface soil (table 9, page 502).

Altho it cannot be definitely stated whether these differences in water-vapor adsorption are due to the effect of drying on the colloidal matter or to the effect of drying on the adsorbed air, if it be assumed that the effect is on the total surface of the soil there is strong evidence of its being more or less permanently diminished by air-drying. In other words, the change due to drying out is not an immediately reversible one.

*Permanency of the effect of drying.*— It was next attempted to ascertain the permanency of this effect of air-drying. Some of the same soils used

in the preceding experiment were kept in air-tight bottles for three months and were then subjected to determinations of hygroscopicity. The results are given in table 12:

TABLE 12. ADSORPTION OF WATER VAPOR BY CONTINUOUSLY MOIST AND BY REMOISTENED SOILS, THREE MONTHS AFTER REMOISTENING

| Soil | Treatment | Per cent of water adsorbed | Difference |
|---|---|---|---|
| Dunkirk surface | Continuously moist | 4.29±0.02 | 0.39±0.02 |
| | Remoistened | 3.90±0.01 | |
| Clyde surface | Continuously moist | 18.80±0.01 | 2.10±0.01 |
| | Remoistened | 16.70±0.01 | |

These data show that after three months the hygroscopicity of the remoistened soils did not return to a value equal to that of the continuously moist soils, indicating that with these soils the effect of drying on this property is not reversible within three months at least.

*Effect of alternate wetting and drying.*—The next experiment was in regard to the effect of alternate wetting and drying. The data are given in table 13:

TABLE 13. EFFECT OF ALTERNATE WETTING AND DRYING OF SOILS UPON THEIR ADSORPTION OF WATER VAPOR

| Soil | Treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|---|
| Dunkirk surface | Continuously moist | 3.97±0.07 | 0.99±0.08 |
| | Air-dried 1 time | 2.98±0.04 | 0.05±0.06 |
| | 2 | 2.93±0.04 | 0.07±0.04 |
| | 4 | 2.86±0.02 | 0.08±0.09 |
| | 8 | 2.78±0.09 | 0.06±0.10 |
| | 16 | 2.84±0.05 | 0.10±0.06 |
| | 32 | 2.94±0.04 | |
| | Difference between 1 drying and 32 dryings | ..... | 0.04±0.06 |

TABLE 13 (*concluded*)

| Soil | Treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|---|
| Clyde surface | Continuously moist | 17.20±0.4 | |
| | Air-dried 1 time | 11.10±0.2 | 6.10±0.4 |
| | 2 | 11.10±0.4 | 0.00±0.4 |
| | 4 | 10.50±0.3 | 0.60±0.5 |
| | 8 | 10.80±0.3 | 0.30±0.4 |
| | 16 | 10.70±0.2 | 0.10±0.4 |
| | 32 | 10.70±0.3 | 0.00±0.4 |
| | Difference between 1 drying and 32 dryings | ..... | 0.40±0.4 |
| Dunkirk subsoil | Continuously moist | 5.97±0.07 | |
| | Air-dried 1 time | 4.11±0.06 | 1.86±0.09 |
| | 2 | 4.10±0.03 | 0.01±0.07 |
| | 4 | 4.02±0.04 | 0.08±0.05 |
| | 8 | 3.95±0.02 | 0.07±0.04 |
| | 16 | 3.86±0.02 | 0.09±0.03 |
| | 32 | 3.80±0.05 | 0.06±0.05 |
| | Difference between 1 drying and 32 dryings | ..... | 0.31±0.08 |
| Vergennes subsoil | Continuously moist | 17.90±0.03 | |
| | Air-dried 1 time | 13.30±0.02 | 4.60±0.04 |
| | 2 | 13.00±0.10 | 0.30±0.10 |
| | 4 | 12.50±0.13 | 0.50±0.16 |
| | 8 | 12.50±0.08 | 0.00±0.14 |
| | 16 | 11.90±0.08 | 0.60±0.11 |
| | 32 | 11.90±0.04 | 0.00±0.09 |
| | Difference between 1 drying and 32 dryings | ..... | 1.40±0.04 |

With all the soils the differences between the percentages of water vapor adsorbed by moist and by air-dried soils are sufficiently great to be significant; but, except in one case — between eight and sixteen dryings of the Vergennes subsoil — the differences between successive dryings are not significant.

Comparing the cumulative effect of thirty-two dryings with the effect of one drying, it is to be seen that the difference is significant with the two subsoils but not with the surface soils. Perhaps the surface soils do not show the cumulative effect because, owing to their natural subjection to the alternate wetting and drying actions, a sort of equilibrium has been established.

No crushing tests were run on these soils, but it was observed while crushing them with the rolling-pin that in general the soils which had been dried the greatest number of times crushed the most easily. This observation agrees with Fippin's (1911) penetration tests on alternately wetted and dried soils.

It was observed also that a mold made its appearance on the Dunkirk and Clyde soils, the two containing the most humus, after about eight wettings and dryings. This is probably due to an increased solubility of the organic matter caused by the treatments.[2]

*Effect of drying at high temperatures.*— Data on the effect of drying at high temperatures are given in table 14:

TABLE 14. ADSORPTION OF WATER VAPOR BY SOILS DRIED AT HIGH TEMPERATURES

| Soil | Treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|---|
| Dunkirk surface | Air-dried | 3.02±0.01 | 0.41±0.02 |
| | Oven-dried | 2.61±0.02 | 1.50±0.02 |
| | Ignited | 1.11±0.01 | |
| Clyde surface | Air-dried | 11.60±0.05 | 1.10±0.05 |
| | Oven-dried | 10.50±0.02 | 5.28±0.04 |
| | Ignited | 5.22±0.03 | |

[2] It is shown later (page 516) that the drying of the soils increases the solubility of their organic matter.

TABLE 14 (*concluded*)

| Soil | Treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|---|
| Dunkirk subsoil | Air-dried | 3.98±0.03 | 0.27±0.04 |
| | Oven-dried | 3.71±0.03 | 0.93±0.04 |
| | Ignited | 2.78±0.03 | |
| Vergennes subsoil | Air-dried | 13.20±0.08 | 0.40±0.09 |
| | Oven-dried | 12.80±0.08 | 3.69±0.04 |
| | Ignited | 9.11±0.02 | |

The following points are shown by the above data: (1) Igniting soils does not destroy their ability to take up moisture from a more or less saturated atmosphere, contrary to frequent assertions that it does. In fact, some of the ignited soils have rather high hygroscopicity. (2) The differences between air-dried and oven-dried conditions are smaller than those between oven-dried and ignited conditions. (3) The hygroscopic values of the soils richest in humus, the surface soils, have suffered the most by ignition.

*Effect of long immersion in water.*— Soils that were continuously air-dried were compared with the same kinds of soils that had been air-dried and then covered with an excess (200 per cent) of water for two years. The soils that had stood under water were again air-dried before being compared with those that were continuously air-dried. The results are given in table 15.

The differences, which are significant in each case, are not in the same direction. The long soaking has increased the adsorptive capacity of the Dunkirk soil, perhaps by a hydrolysis of the inorganic constituents, producing the colloidal condition.

The decrease in the adsorptive capacity of the Clyde soil can be accounted for by the decomposition of the colloidal organic matter, which was contained in this soil to a greater extent than in the Dunkirk soil. This decrease in colloidal content may override any increase thru

hydrolysis. It was observed that bacterial activity, as judged by the appearance of gases, was especially great in the Clyde soil. That previous drying of a soil increases its bacterial activity has been shown by Klein (1915) and by others.

TABLE 15. ADSORPTION OF WATER VAPOR BY SOILS IMMERSED IN WATER FOR TWO YEARS

| Soil | Treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|---|
| Dunkirk surface | Air-dried | 2.77±0.02 | 0.13±0.02 |
| | Under water | 2.90±0.01 | |
| Clyde surface | Air-dried | 10.50±0.003 | 0.40±0.005 |
| | Under water | 10.10±0.004 | |

*Effect of leaching.*— The effect of leaching on the colloidal content of soils is of more importance than the amount of work done on this point would indicate. It was studied only briefly. The data are presented in table 16:

TABLE 16. ADSORPTION OF WATER VAPOR BY LEACHED AND BY UNLEACHED SOIL

| Soil treatment | Per cent of water vapor adsorbed | Difference |
|---|---|---|
| Leached | 4.46±0.01 | 1.44±0.02 |
| Unleached | 3.02±0.02 | |

### *Dye-adsorption experiments*

The dye-adsorption experiments were carried on with the same kinds of soils and some of the same treatments as have already been mentioned in connection with water-vapor-adsorption experiments.

Data showing the effect of alternate wetting and drying of soils on their adsorption of methylene blue are presented in table 17:

TABLE 17. EFFECT OF ALTERNATE WETTING AND DRYING OF SOILS ON THEIR ADSORPTION OF METHYLENE BLUE

| Soil | Treatment | Corrected colorimetric reading | Milligrams of dye adsorbed per gram of soil | Difference |
|---|---|---|---|---|
| Dunkirk surface | Continuously moist.... | 53.5±1.7 | 4.870±0.004 | |
| | Air-dried 1 time..... | 135.0±1.4 | 4.950±0.0005 | 0.080±0.004 |
| | 2 ..... | 125.0±2.4 | 4.945±0.001 | 0.005±0.001 |
| | 4 ..... | 133.0±2.4 | 4.950±0.001 | 0.005±0.001 |
| | 8 ..... | 133.0±4.1 | 4.950±0.002 | 0.000±0.002 |
| | 16 ..... | 138.0±2.0 | 4.950±0.0005 | 0.000±0.002 |
| | 32 ..... | 131.0±2.4 | 4.950±0.001 | 0.000±0.001 |
| | Oven-dried once..... | 88.0±0.0 | 4.920±0.000 | 0.030±0.001 |
| | Ignited..... | 6.8±0.1 | 3.985±0.015 | 0.935±0.015 |
| | Difference between 1 drying and 32 dryings | ..... | ..... | 0.000±0.001 |
| Clyde surface | Continuously moist.... | 50.5±0.2 | 9.97±0.000 | |
| | Air-dried 1 time..... | 115.8±0.6 | 9.99±0.000 | *0.02±0.000 |
| | 2 ..... | 133.0±0.6 | 9.99±0.000 | 0.00±0.000 |
| | 4 ..... | 155.8±2.6 | 9.99±0.000 | 0.00±0.000 |
| | 8 ..... | 146.0±2.0 | 9.99±0.000 | 0.00±0.000 |
| | 16 ..... | 140.2±4.8 | 9.99±0.000 | 0.00±0.000 |
| | 32 ..... | 151.5±2.2 | 9.99±0.000 | 0.00±0.000 |
| | Oven-dried once..... | 92.8±0.6 | 9.98±0.000 | 0.01±0.000 |
| | Ignited..... | 3.1±0.0 | 9.53±0.030 | 0.45±0.030 |
| | Difference between 1 drying and 32 dryings | ..... | ..... | 0.00±0.000 |

* In cases when the probable error of the mean is 0.000, separate determinations were so close as to make it negligible.

TABLE 17 (*concluded*)

| Soil | Treatment | Corrected colorimetric reading | Milligrams of dye adsorbed per gram of soil | Difference |
|---|---|---|---|---|
| Dunkirk subsoil | Continuously moist.... | 52.9 ±0.8 | 9.91±0.002 | |
| | | | | 0.09±0.003 |
| | Air-dried 1 time..... | 26.0 ±0.0 | 9.82±0.002 | |
| | | | | 0.02±0.003 |
| | 2 ..... | 28.9 ±0.1 | 9.84±0.002 | |
| | | | | 0.00±0.004 |
| | 4 ..... | 28.6 ±0.3 | 9.84±0.003 | |
| | | | | 0.00±0.004 |
| | 8 ..... | 28.3 ±0.4 | 9.84±0.003 | |
| | | | | 0.00±0.004 |
| | 16 ..... | 29.4 ±0.3 | 9.84±0.003 | |
| | | | | 0.00±0.009 |
| | 32 ..... | 28.25±0.7 | 9.84±0.009 | |
| | | | | 0.11±0.010 |
| | Oven-dried once..... | 17.0 ±0.2 | 9.73±0.005 | |
| | | | | 2.88±0.041 |
| | Ignited..... | 1.5 ±0.0 | 6.85±0.041 | |
| | Difference between 1 drying and 32 dryings | ..... | ..... | 0.02±0.009 |
| Vergennes subsoil | Continuously moist.... | 54.9 ±1.9 | 39.90±0.004 | |
| | | | | 0.00±0.004 |
| | Air-dried 1 time..... | 54.75±0.7 | 39.90±0.000 | |
| | | | | 0.00±0.000 |
| | 2 ..... | 54.75±0.7 | 39.90±0.000 | |
| | | | | 0.00±0.000 |
| | 4 ..... | 61.4 ±0.5 | 39.90±0.000 | |
| | | | | 0.02±0.000 |
| | 8 ..... | 50.4 ±0.8 | 39.88±0.000 | |
| | | | | 0.05±0.000 |
| | 16 ..... | 81.5 ±1.6 | 39.93±0.000 | |
| | | | | 0.05±0.000 |
| | 32 ..... | 93.4 ±2.6 | 39.98±0.000 | |
| | | | | 0.22±0.000 |
| | Oven-dried once..... | 24.0 ±0.3 | 39.76±0.000 | |
| | | | | 31.88±0.000 |
| | Ignited..... | 0.2 ±0.0 | 7.88±0.000 | |
| | Difference between 1 drying and 32 dryings | ..... | ..... | 0.08±0.000 |

These results are rather irregular, and, on the whole, inconsistent. With the two surface soils there is an increase in their adsorptive capacities due to one air-drying, a result just opposite to that obtained by the water-vapor-

adsorption method. The Dunkirk subsoil shows a decrease in adsorptive capacity due to one air-drying, and the Vergennes soil shows no effect.

The differences between successive dryings are in many cases significant, but the results are so erratic as to justify no conclusions. With the two surface soils the cumulative effect of thirty-two dryings is nil, but with the two subsoils the cumulative effect is great enough to be significant in one case. This last observation is not in accord with the one on the same point under hygroscopicity.

The effects of oven-drying and ignition are very marked in all cases, there being a decrease in adsorption in going from the air-dry to the oven-dry and to the ignited conditions. The differences are more marked with the subsoils than with the surface soils.

A point which stands out in comparing the results obtained by this method with those obtained from the water-vapor-adsorption method is that the Clyde soil shows the least changes in its adsorptive capacity due to drying. Even the ignited Clyde soil adsorbs nearly as much as the same soil under other conditions.

As already stated, a glacial clay subsoil was thrown out of the hygroscopicity experiments because of its unusual adsorptive capacity. This soil was subjected to dye-adsorption tests. The results are given in table 18:

TABLE 18. ADSORPTION OF METHYLENE BLUE BY A GLACIAL CLAY SUBSOIL VARIOUSLY TREATED

| Soil treatment | Corrected colorimetric reading | Milligrams of dye adsorbed per gram of soil | Difference |
|---|---|---|---|
| Continuously moist | 50.0 ±0.1 | 19.88±0.002 | |
| | | | 0.05±0.002 |
| Air-dried 1 time | 35.6 ±0.5 | 19.83±0.002 | |
| | | | 0.03±0.002 |
| 8 | 30.25±0.3 | 19.80±0.002 | |
| | | | 0.01±0.002 |
| 16 | 30.9 ±0.3 | 19.81±0.002 | |
| | | | 0.02±0.004 |
| 32 | 28.5 ±0.6 | 19.79±0.004 | |
| | | | 0.00±0.004 |
| Oven-dried once | 20.25±0.1 | 19.79±0.002 | |
| Difference between 1 drying and 32 dryings | ..... | ..... | 0.04±0.004 |

The differences between successive drying treatments are significant in every case except between air-drying and oven-drying, but the changes due to successive air-drying are not always in the same direction. The cumulative difference due to thirty-two dryings as compared with one drying is significant. The results are not wholly in accord with those of other soils similarly treated.

In table 19 are given the effects of long immersion of soils on their adsorptive capacity for methylene blue:

TABLE 19. ADSORPTION OF METHYLENE BLUE BY SOILS IMMERSED IN WATER FOR TWO YEARS

| Soil | Treatment | Corrected colorimetric reading | $(C-C_1)$ · dye adsorbed per gram of soil | Difference |
|---|---|---|---|---|
| Dunkirk surface | Air-dried | 25.0±0.1 | 60.0±0.16 | 14.4±0.21 |
| | Under water | 39.1±0.2 | 74.4±0.13 | |
| Clyde surface | Air-dried | 51.9±0.6 | 80.7±0.22 | 8.6±0.22 |
| | Under water | 93.5±0.4 | 89.3±0.04 | |

The long soaking under water has increased the adsorptive capacities of these soils. The results with the Dunkirk soil agree with those obtained by water-vapor adsorption, while those with the Clyde soil do not.

Adsorption of methylene blue by leached and by unleached soil is shown by table 20:

TABLE 20. ADSORPTION OF METHYLENE BLUE BY LEACHED AND BY UNLEACHED SOIL

| Soil treatment | Corrected colorimetric reading | $(C-C_1)$ · dye adsorbed per gram of soil | Difference |
|---|---|---|---|
| Leached | 189.0±3.0 | 94.7±0.84 | 8.2±0.84 |
| Unleached | 74.1±0.3 | 86.5±0.06 | |

Leaching has increased the adsorptive capacity of this soil for this dye. The results agree with those obtained by the water-vapor-adsorption method.

Owing to the opposite behavior of the diamine sky-blue with the different artificially prepared colloidal materials as compared with methylene blue, it was decided to ascertain the effect of moisture changes on the capacity of the soils for this dye. The results are given in table 21:

TABLE 21. EFFECT OF DRYING SOILS ON THEIR ADSORPTION OF DIAMINE SKY-BLUE

| Soil | Treatment | Corrected colorimetric reading | Milligrams of dye adsorbed per gram of soil | Difference |
|---|---|---|---|---|
| Dunkirk surface | Continuously moist.. | 52.00±0.7 | 0.42±0.008 | |
| | Air-dried once..... | 47.40±0.5 | 0.37±0.007 | 0.05±0.011 |
| | Oven-dried once..... | 75.40±0.6 | 0.61±0.003 | 0.24±0.008 |
| | Ignited..... | 71.50±1.4 | 0.58±0.008 | 0.03±0.009 |
| Clyde surface | Continuously moist.. | 49.75±0.4 | 0.78±0.026 | |
| | Air-dried once..... | 73.10±0.8 | 1.21±0.018 | 0.43±0.032 |
| | Oven-dried once..... | 71.75±1.0 | 1.19±0.020 | 0.02±0.027 |
| | Ignited..... | 45.60±0.8 | 0.73±0.034 | 0.46±0.039 |
| Dunkirk subsoil | Continuously moist.. | 49.25±2.0 | 4.16±0.035 | |
| | Air-dried once..... | 56.10±0.6 | 4.26±0.010 | 0.10±0.036 |
| | Oven-dried once..... | 60.25±1.2 | 4.31±0.015 | 0.05±0.018 |
| | Ignited..... | 42.50±1.2 | 4.02±0.030 | 0.29±0.035 |
| Vergennes subsoil | Continuously moist.. | 48.25±0.9 | 3.81±0.035 | |
| | Air-dried once..... | 76.00±1.6 | 4.24±0.025 | 0.43±0.042 |
| | Oven-dried once..... | 70.40±0.7 | 4.18±0.020 | 0.06±0.032 |
| | Ignited..... | 11.95±0.3 | 0.17±0.150 | 4.01±0.163 |

The effect of air-drying once was to decrease the adsorption by the Dunkirk surface soil and to increase it with the other soils. As between

the air-dry and the oven-dry condition, there is an increase with one surface soil and one subsoil, and a decrease with the other two; the differences are significant, however, with one soil only, the Dunkirk surface soil. Between the oven-dried and the ignited condition there is a decrease which is significant in every case but one. The only point which stands out clearly is that ignition decreases the adsorption of this dye. By comparing the results with those given in table 17 (page 510–511), it is seen that all these soils adsorb less of this dye than of methylene blue.

*Suspension experiments*

The suspension method is described on page 499. The results of the experiments with this method are given in table 22:

TABLE 22. PER CENT OF CLYDE SOIL REMAINING IN SUSPENSION IN DISTILLED WATER THIRTY MINUTES AFTER SHAKING

| Soil treatment | In distilled water | In 4-per-cent ammonia |
|---|---|---|
| Continuously moist | 9.15 | 21.90 |
| Air-dried 1 time | 6.55 | 17.10 |
| 16 | 3.40 | 7.35 |
| 32 | 3.70 | 7.75 |
| Oven-dried once | 4.80 | 9.45 |

In both distilled water and ammonia the moist soil was deflocculated the most, and the soil that was air-dried once was deflocculated more than those that were air-dried sixteen or thirty-two times. The deflocculating influence of the ammonia was very marked. These results show that the flocculated condition is not immediately reversible, even with shaking in water.

*Additional experiments*

Owing to the striking influence of drying on the colloidal matter of the Clyde soil, as shown by the experiments in water-vapor adsorption and as mentioned in the literature, it was thought probable that differences in the amount of humus extractable by ammonia could be found. With

this in mind an experiment was planned. The method used is described on page 502. The results are given in table 23:

TABLE 23. EFFECT OF ALTERNATE WETTING AND DRYING UPON THE AMOUNT OF HUMUS EXTRACTED FROM A CLYDE SOIL

| Soil treatment | Per cent of humus extracted |
|---|---|
| Continuously moist | 4.40 |
| Air-dried 1 time | 4.42 |
| 2 | 4.44 |
| 4 | 4.34 |
| 8 | 4.48 |
| 16 | 4.18 |

The differences are not great enough to warrant drawing a conclusion that the moisture changes affected the amount of humus extracted by this method. It is very likely that the treatment, as the purpose for which it was designed would lead one to believe, took out all the humus. The extraction by this method is probably so thoro as to mask any small differences that might exist as a result of moisture changes.

The data given in table 24 were obtained by comparing, colorimetrically, distilled water extracts, which were filtered thru a porcelain filter. The

TABLE 24. RELATIVE INTENSITIES OF WATER EXTRACTS OF DUNKIRK AND CLYDE SURFACE SOILS

| Soil | Moist | Air-dried | Difference |
|---|---|---|---|
| Dunkirk surface | 50 | 20.8±2.5 | 29.2±2.5 |
| Clyde surface | 50 | 9.0±0.7 | 41.0±0.7 |

results show that air-drying these soils has increased the solubility of the coloring matter of the humus, if not the humus itself.

This increase in solubility of humus material probably accounts in a measure for the growth of molds, after several wettings and dryings, on the soils that contained humus.

*Chemical nature of soil colloids*

During the course of the experiments in which the soil was allowed to stand with an excess of water, it was frequently observed that a colloidal material of the appearance of ferric oxide was obtained. In some cases the similarity to ferric hydrate was very marked, and in other cases the material had only a rusty stain.

It was felt that this was, in part at least, colloidal ferric hydrate, and that it was caused by bacterial decomposition of the organic matter of the soils, and solution and hydration of the released salts.

Dye-adsorption tests failed to show any significant differences. It was thought that diamine sky-blue, which had been found to be strongly adsorbed by artificially prepared colloidal ferric oxide, would show differences. It did not, however. It is very likely that the organic matter in the soil is more or less adsorbed by the ferric oxide and that it acts as a protective colloid, preventing the adsorption of an acid dye.

It was decided to try the solubility of this material in weak hydrochloric acid. Accordingly, the soils were shaken with approximately N/30 hydrochloric acid, allowed to stand for a while, and then filtered. In the filtrate iron was determined by the colorimetric method given in Bulletin 1 of the United States Bureau of Soils. The results are given in table 25:

TABLE 25. EFFECT OF DIFFERENT TREATMENTS ON THE SOLUBILITY OF IRON IN WEAK HYDROCHLORIC ACID

(Expressed in parts per million)

| Soil | Soil standing in 200 per cent of water | | | | Fresh oven-dried |
|---|---|---|---|---|---|
| | Moist | Air-dried | Oven-dried | Oven-dried and sterile | |
| Dunkirk surface | Trace | 1.3 | 55.6 | 4.6 | 3.1 |
| Clyde surface | 26.6 | 26.4 | 42.75 | Trace | Trace |
| Bergennes subsoil | Trace | Trace | Trace | Trace | Trace |
| Cecil subsoil | ..... | ..... | 8.0 | ..... | Trace |

It is seen that oven-drying these soils previous to their standing in water increased the amount of easily soluble iron, and that sterilization

of the soils inhibited the formation of these easily soluble compounds. These results agree with the appearance of the soils.

One way to account for these effects is by bacterial activity. Some investigators have shown that oven-drying a soil increases the solubility of the organic matter but does not appreciably affect the iron compounds.

Oven-drying does not kill all bacteria. Owing to the increased food in the water with the oven-dried soil, the bacteria may work more vigorously and destroy the organic matter. Thus adsorbed iron compounds may be liberated directly, or indirectly as products of excretion. In any event, more iron compounds may be brought into solution thru bacterial destruction of the organic matter. These may hydrolyze and form colloidal ferric hydrate.

Ellis (1915) has observed this formation of ferric hydrate in many waters and has accounted for its formation by the action of special iron-bacteria. He admits, however, that the action is not limited strictly to these iron-bacteria, but that others may bring it about. It seems more reasonable to assume, therefore, that the part the bacteria play is in regard to breaking down the organic matter. This was suggested by Brown (quoted by Ellis, 1915).

That the iron compound probably first appears as crystalloidal is indicated by the manner in which it usually forms in the supernatant liquid. Its crystalloidal character was further indicated by an experiment in which some of the dried soil was placed in a collodion dialyzing sack with some distilled water, the sack then being immersed in distilled water. The colloidal precipitate was later found outside the sack as well as inside. The assumption is that part of the iron compound must have gone thru the membrane as a crystalloid and later was hydrolyzed and precipitated, for the colloidal form will not pass thru the membrane. The identity of the colloidal ferric oxide outside the membrane was established by dissolving it in weak hydrochloric acid and testing qualitatively.

## SUMMARY

The experimental work here presented may be summarized as follows:

Variations of from 5 to 10 degrees between 15° and 40° C. did not materially affect the adsorption of water vapor.

The chemical composition of certain soil-forming minerals affected the adsorption of dyes. Acid dyes, as a rule, were more strongly adsorbed

by basic minerals than were basic dyes; and basic dyes were more strongly adsorbed by acid minerals.

Diamine sky-blue was one of the few dyes strongly adsorbed by colloidal ferric oxide, and, of all those examined, was adsorbed the most strongly. It was adsorbed also by alumina, but not by silica.

An alga and a fungus adsorbed considerable amounts of the dyes used in soil-adsorption work. The growth in soils of lower forms of plant life affects the adsorptive capacity of the soil.

Air-dried and oven-dried colloidal silica, alumina, ferric oxide, and humus, immersed in dye solutions, showed a reversal of their capacity to adsorb dyes. They also adsorbed water vapor rapidly.

The difference in hygroscopicity between a moist and an air-dried soil persists for three months at least.

Remoistening air-dried soils to a content of moisture above that originally held did not cause a reversal of hygroscopicity immediately, nor within three months.

Alternate wetting and drying of soils did not affect the hygroscopicity after the first drying. With the subsoils that had been wetted and dried thirty-two times there was a cumulative decrease in hygroscopicity which was significant.

Hygroscopicity was decreased successively by air-drying, oven-drying, and ignition. The change from the moist to the air-dry condition produced a greater change than that from the air-dry to the oven-dry; and from the oven-dry to the ignited condition the change was greater than from the air-dry to the oven-dry condition. Some ignited soils had comparatively high hygroscopic values.

Long immersion under water increased the hygroscopicity of a soil poor in organic matter, and decreased it in one rich in organic matter.

Leaching a soil raised its capacity for adsorbing water vapor.

Oven-drying and ignition reduced the adsorption of methylene blue. The Clyde soil, rich in organic matter, showed less effect due to drying than did the other soils. This was contrary to results with water-vapor adsorption. Effects of air-drying and alternate wetting and drying were so irregular, as measured by dye adsorption, as to be inconclusive.

Immersion of a soil in water for two years increased its adsorptive capacity for methylene blue.

Leaching a soil increased its adsorption of methylene blue.

Experiments with the adsorption of diamine sky-blue showed that less of the dye was adsorbed than of methylene blue. The only point that stood out clearly, as regards moisture changes, was that ignition decreased the adsorption of this dye.

Drying a soil decreased the amount of it that would go into suspension in distilled water and in 4-per-cent ammonium hydroxide. Drying thirty-two times as compared with drying one time decreased the amount of suspended matter.

Extractions of humus with 4-per-cent ammonium hydroxide showed no effect on humus due to drying.

Extractions with distilled water showed an increase in the solubility of the coloring matter of humus due to drying.

Oven-drying soils previous to their standing in an excess of water increased the amount of iron soluble in weak hydrochloric acid. Sterilization checked the formation of this easily soluble colloidal material.

Judged by the consistency of the results, the water-vapor-adsorption method is better than the dye-adsorption method for measuring the total surface of soils.

## GENERAL CONCLUSIONS

Drying a surface soil once produces as much effect on the colloidal material as repeated dryings alternated with moistenings.

With a subsoil there is a cumulative effect due to alternate drying and wetting.

Drying a soil once or many times produces a change in the colloidal material from which it does not immediately recover on being wetted.

Drying a soil affects indirectly the reversibility of its colloidal condition, the changes being directly produced thru biological and chemical action.

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# AN ANALYSIS OF THE COSTS OF GROWING POTATOES

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# AN ANALYSIS OF THE COSTS OF GROWING POTATOES

# AN ANALYSIS OF THE COSTS OF GROWING POTATOES[1]

D. S. Fox

New York farmers receive more money for potatoes than for any other crop. The average annual acreage for the ten-years period from 1906 to 1915 was 396,400 acres (table 1); the average annual production was 38,575,200 bushels, worth $22,917,100. About seven-eighths of the potatoes are sold from the farm. Practically all of these are used for human food.

TABLE 1. Potato Acreage, Production, and Value, in New York, 1906–1915*

| Year | Acreage | Production (bushels) | Value |
|---|---|---|---|
| 1906 | 420,000 | 44,143,000 | $21,630,000 |
| 1907 | 426,000 | 41,748,000 | 23,796,000 |
| 1908 | 425,000 | 34,850,000 | 26,138,000 |
| 1909 | 438,000 | 52,560,000 | 26,280,000 |
| 1910 | 438,000 | 44,676,000 | 21,444,000 |
| 1911 | 375,000 | 27,750,000 | 24,975,000 |
| 1912 | 360,000 | 38,160,000 | 22,133,000 |
| 1913 | 360,000 | 26,640,000 | 21,312,000 |
| 1914 | 367,000 | 53,215,000 | 23,415,000 |
| 1915 | 355,000 | 22,010,000 | 18,048,000 |
| Total, 1906–1915 | 3,964,000 | 385,752,000 | $229,171,000 |

* The figures are taken from the Yearbooks of the United States Department of Agriculture for the ten years from 1906 to 1915, inclusive.

The acreage devoted to potatoes in New York State has decreased materially since 1906, as shown in table 1. In the same period the acreage in the United States has increased. The reduction of the acreage of potatoes in New York is an expression of the readjustment that is con-

[1] Also presented to the Faculty of the Graduate School of Cornell University, October, 1916, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

Author's Acknowledgment. The writer is indebted to Professor G. F. Warren, under whose direction this investigation was conducted, and to Professor K. C. Livermore, for many valuable suggestions and criticisms. The data were collected by a field party consisting of E. V. Hardenburg, W. M. Peacock, M. F. Abell, R. H. Cross, and the writer. The investigation was made possible by the willing cooperation of the many New York farmers who furnished the data.

stantly taking place in American agriculture. Since 1896 the wholesale price of potatoes in comparison with the average wholesale price of five important farm crops and five important animal products has been relatively lower than for the twenty years preceding that date (fig. 77). This reduction in relative price has made potatoes a less desirable crop in New

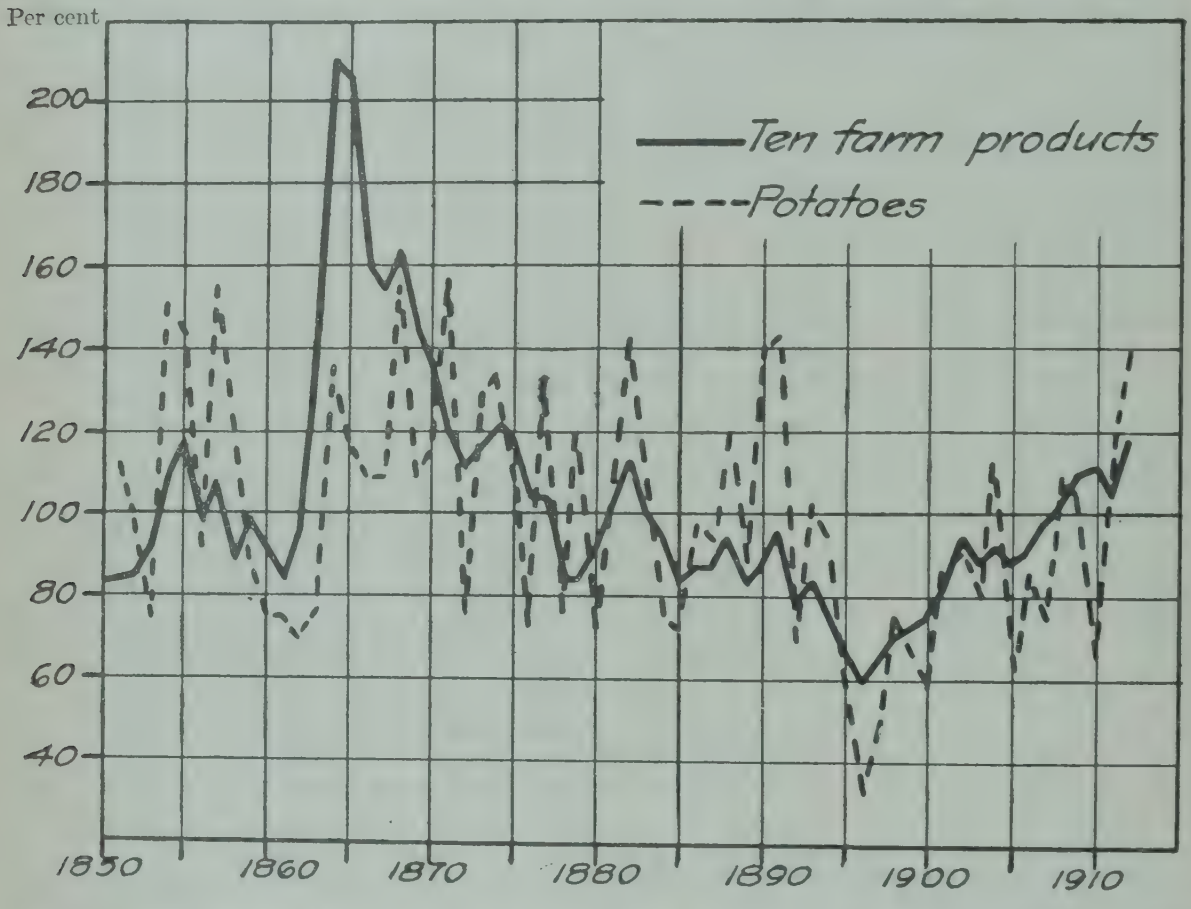


FIG. 77. AVERAGE WHOLESALE PRICES IN CITIES FOR FIVE IMPORTANT FARM CROPS AND FIVE IMPORTANT ANIMAL PRODUCTS, AND FOR POTATOES

The average for seventy-three years (from 1840 to 1912) equals 100 per cent. The price of potatoes in relation to the average prices of ten farm products has been lower since 1896 than for the twenty years preceding that date

York. Consequently potato production is shifting to sections more favorable to the industry, and New York farmers are replacing potatoes with more profitable crops. However, New York will always be a great potato-growing State, owing to its nearness to centers of dense population and to the lack of a more profitable competing crop in many of its potato-growing sections.

## SCOPE OF THE WORK

### *Purpose*

This investigation was conducted for the purpose of obtaining more definite and accurate knowledge of the cost of growing potatoes, and in order to study the factors influencing their profitable production.

### *Methods*

The data for the investigation were collected by two methods, survey and cost accounting.

In gathering the data by the survey method, each farmer in the region studied who grew a certain acreage of potatoes was visited and the data were obtained directly from him. A blank similar to that shown on pages 624 to 627 was used. The blank used in the field had spaces for only those questions that were asked the farmer. These data were copied each evening on an office blank and the transfer was carefully checked. Records that were not complete were finished when possible or were discarded. Practically the same statistical methods were used as in previous surveys made by the Department of Farm Management of the New York State College of Agriculture.

The cost-account data were taken from complete sets of cost accounts for twenty-six New York farms, kept by the Department of Farm Management at the College in cooperation with the Office of Farm Management at Washington, D. C. The hours of labor, the receipts, and the expenses were recorded day by day. For individual farms such records are more accurate than survey records, but the much higher cost of obtaining them makes it impracticable to get a large number. Because of the smaller number of records, the cost-account results are probably less representative of the costs and profits of growing potatoes in New York than the results from the survey data.

### *Accuracy*

The accuracy of work of this kind depends primarily on the person who asks the questions and how they are asked. If the questions are asked in detail the farmer can give accurate answers. He remembers the time required to plow or to plant a certain field. He remembers the number

of men and horses used and the time required to dig a certain field of potatoes. When large numbers of farms are used, the average for any one factor will be more accurate than the same factor for any individual record.

The probable error for any series of observations is expressed by the formula $\pm 0.6745\sqrt{\frac{\Sigma D^2}{n(n-1)}}$, in which $\Sigma D^2$ is the sum of the squares of the differences of the various observations from the mean of all observations, without regard to the sign, and $n$ is the number of observations. The probable errors in some of the more important data from Steuben, Suffolk, and Nassau Counties are given in connection with the data.

### *Location of the areas studied*

In the summer of 1913, surveys were conducted in three regions by the Department of Farm Management of the State College of Agriculture in cooperation with the Department of Farm Crops, and data were obtained for the 1912 crop. These data, which are given in table 2, include records from 355 farms in northern Steuben County, 161 farms in eastern

TABLE 2. Potato Production in the Areas Studied

| Location of area | Year | Number of records | Acres in potatoes | Acres in potatoes per farm |
|---|---|---|---|---|
| Steuben County | 1912 | 355 | 5,227.1 | 14.7 |
| Suffolk County | 1912 | 161 | 3,149.7 | 19.6 |
| Nassau County | 1912 | 41 | 1,466.3 | 35.8 |
| Clinton and Franklin Counties | 1913 | 300 | 2,160.0 | 7.2 |
| Cost-account farms | 1913–14–15 | 26 | 338.5 | 13.0 |

Suffolk County, and 41 farms in Nassau County. The survey in Clinton and Franklin Counties, as summarized in a thesis by W. M. Peacock in the Cornell University Library, includes records from 300 farms in northeastern Franklin County and central and northwestern Clinton County for the year 1913. The cost-account data include records for one or more crops of potatoes on 20 farms, 26 crops in all. The farms are located in the central and western parts of the State. Nine of the cost-account records are for the season of 1913, nine are for 1914, and eight are for 1915.

The location of the areas studied is shown in figure 78.

FIG. 78. LOCATION OF AREAS STUDIED

## COST OF POTATO PRODUCTION ON 355 FARMS IN STEUBEN COUNTY, 1912

### *Description of the region*

The region studied in Steuben County is located in the northern part of the county. The topography is similar to that of most of south central New York, consisting of a broad, rolling plateau, cut by narrow valleys which gradually become wider and deeper as they approach the main river valley (fig. 79). A large proportion of the potatoes were grown on the more or less level plateau land and on the valley sides. Seventy-six per cent of the farms studied had an elevation of 1500 feet or more, and six per cent were above 2000 feet.

The soils on the farms studied are largely Lordstown loam on the hillsides and a light phase of Lordstown silt loam on the plateau land. There is some Chenango loam on the river bottoms and some Volusia

silt loam at an elevation of from 1800 to 2000 feet near the southern edge of the region. All the farms had some small flat stones, but usually not in sufficient quantity to interfere with the operation of machinery. Most of the land is naturally well drained. Altho the soil is better supplied with lime than are the Volusia soils farther south, it was sufficiently acid to prevent trouble with scab. The growth of clover was only fair.

The length of the growing season varies from 120 to 140 days, which is nearly the same as for Clinton and Franklin Counties and from 30 to 80

FIG. 79. A VIEW OF THE COHOCTON VALLEY

The broad rolling table-land with narrow intersecting valleys is typical of northern Steuben County

days shorter than the growing season on Long Island. The average rainfall for April to August inclusive varies from 16 to 18 inches.

The farms studied grew 5 or more acres of potatoes. The average size of these farms was 146 acres, of which 80.6 acres, or 55.2 per cent, was in crops. The average acreage in potatoes per farm was 14.7 acres. Next to Long Island this region is one of the most intensive potato-growing sections of the State. On the farms studied, 18 per cent of the crop land was devoted to potatoes, 42 per cent to hay, 22 per cent to oats, 4 per cent to buckwheat, 3 per cent to rye, and 3 per cent to wheat.

Fig. 80. A TYPICAL POTATO FIELD ON THE STEUBEN COUNTY PLATEAU

Fig. 81. POTATOES IN STEUBEN COUNTY ON LAND WHICH IS TOO STEEP FOR THE USE OF IMPROVED MACHINERY

### *Seed*

The average cost of seed used per acre on the farms in Steuben County was $9.48, as shown in table 3. The average price of the seed per bushel

TABLE 3. QUANTITY AND COST OF SEED, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Total | Average per acre |
|---|---|---|
| Bushels used | 53,109 | 10.2 |
| Cost | $49,539 | $9.48 |

was 93 cents, which was almost twice the normal price for the quality of seed used. Probably more and better seed would have been used if the price had been normal. The amount of seed used per acre varied from 6 to 18.4 bushels. Seven farms used less than 7 bushels, and eighteen farms used more than 14 bushels, per acre.

### *Manure*

A very few farmers left a poor crop of hay or weeds to be plowed under for potatoes. This was the nearest approach to green manure on the farms studied. This hay was not taken into account in computing the cost. As such a crop was usually plowed under on the poorest fields, and as the crop was generally small, the error is negligible.

Stable manure was used for potatoes on 332 of the 355 farms. On 331 farms the manure was applied directly to the crop. On the remaining farm the manure was applied to corn preceding potatoes.

The manure was estimated to be worth $1.50 per ton plus the man and horse labor and the equipment cost of application. As the benefits from an application of manure extend over a period of years, it was estimated that potatoes received 40 per cent of the value of all stable manure applied directly to the potato land, and 30 per cent of the value of manure applied to the crop preceding potatoes in the rotation. A total of 29,925.5 tons of manure was applied directly to 2560.6 acres of potatoes at an average rate of 11.7 tons per acre, and 75 tons was applied to 5 acres of corn preceding potatoes. According to the above statement the potato crop should pay for 11,992.7 tons of manure. The average cost of this manure

for each acre receiving the benefit of the application was $9.77, and for each acre of the entire acreage in potatoes it was $4.80 (table 4).

TABLE 4. QUANTITY AND COST OF MANURE USED, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Total | Average per acre for all farms |
|---|---|---|
| Tons used by potatoes | 11,992.7 | 2.3 |
| Cost | $25,064 | $4.80 |

*Fertilizer*

On 147 farms fertilizer was used on 1500 acres of potatoes. A total of 649,440 pounds was applied, or an average of 433 pounds per acre for the farms using the fertilizer. The average application for the entire acreage in potatoes was 124 pounds per acre (table 5). The average price of the fertilizer at the railway station was $26.72 per ton.

TABLE 5. QUANTITY AND COST OF FERTILIZER USED, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Total | Average per acre for all farms |
|---|---|---|
| Pounds used | 649,440 | 124 |
| Cost | $8,675 | $1.66 |

*Spray materials*

Potatoes were sprayed on 180 of the 355 farms. Only 17 farms sprayed with bordeaux. The average cost per acre for copper sulfate and lime on these farms was $1.10. Arsenical poison for Colorado potato beetle was used on 175 farms. The average cost of insecticide per acre on these farms was 24 cents. Traction sprayers were used on 43 farms. A majority of the remaining farms used hand sprayers, which consisted of a quart can attached to the end of a hand-pump cylinder. The total and average cost of the spray materials used is given in table 6:

TABLE 6. Cost of Spray Materials Used, 355 Farms, 5227.1 Acres, Steuben County, 1912

| | Total cost | Average cost per acre for all farms |
|---|---|---|
| Fungicides | $395 | $0.08 |
| Insecticides | 637 | 0.12 |
| Total cost of spray materials | $1,032 | $0.20 |

The insecticide used by most farmers was paris green. A considerable amount of arsenate of lead also was used. Arsenite of soda was little used, notwithstanding its cheapness. Many farmers reported that it burned the vines severely. Some farmers added lime to the insecticide solution to neutralize any free arsenic.

Attacks of late blight are not so frequent in this section as in parts of the State lying at a lower elevation. The small number of farmers who sprayed with bordeaux indicates that the majority of farmers regard it as an insurance of doubtful profit.

The kinds of spray materials used are given in table 7:

TABLE 7. Kinds of Spray Materials Used, 355 Farms, 5227.1 Acres, Steuben County, 1912

| Material | Quantity (pounds) | Cost |
|---|---|---|
| Insecticides | | |
| Paris green | 2,167 | $501 |
| Arsenate of lead | 1,086 | 112 |
| Arsenite of soda | ..... | 11 |
| Lime | 1,050 | 13 |
| Fungicides | | |
| Copper sulfate | 4,980 | 346 |
| Lime | 7,010 | 49 |
| Total cost | ..... | $1,032 |

*Land rental*

Adequate information to fix the land rental for each farm was not obtained. The survey data showed that the average value of the crop

land without buildings was approximately $50 per acre. Allowing 5 per cent for interest and 1 per cent for taxes and upkeep, the rental of the land would be $3 per acre. This rental was used on all farms in calculating the cost of production. Only 8 per cent of the cost of growing potatoes was for land rental. An increase of $25 in the value per acre of crop land would add only $1.50 per acre to the rental. It would seem, then, that in potato production, land would be one of the last items in which to economize. The total cost for use of land was $15,681.

### *Use of buildings*

The cost data for use of buildings were not obtained for all farms. On the cost-account farms this cost averaged one cent for each bushel stored. This was the figure used in computing the use-of-buildings cost in Steuben County, which is shown in table 8:

TABLE 8. COST FOR USE OF BUILDINGS, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | |
|---|---|
| Bushels stored | 421,815 |
| Total cost for use of buildings | *$4,226.00 |
| Cost per acre for use of buildings | $0.81 |
| Cost per bushel stored for use of buildings | $0.01 |

* The apparent discrepancy between the number of bushels stored and the cost of storage is due to the statistical method used. In figuring the total cost of production on a farm, all total cost figures were carried to the nearest even dollar. Thus, in the 355 records, $8 was added to the cost of storage.

The usual storage place was the cellar of the farmhouse. Some potatoes were stored temporarily in basements of the farm barns. Nine farmers had special storage houses, usually cellars with heavy walls, under granaries or other farm buildings.

### *Labor*

The most important cost item in the production of potatoes was labor. The cost of man and horse labor represented 61 per cent of the cost of growing and marketing. This included all the labor on the crop except that of applying manure.

Information concerning the wages paid for hired help was obtained for each farm. It was impossible, however, to ascertain the number of hours worked per month, and thus it was impossible to compute the cost per

hour. On the cost-account farms the hours of labor as well as the total costs are known. The cost per hour of man labor on these farms averaged from 15 to 18 cents. After comparing the wages paid for hired help on the farms in Steuben County with the wages paid on the cost-account farms, it seemed fair to estimate the cost of man labor at $17\frac{1}{2}$ cents per hour. This rate includes the value of board furnished the helpers, and the value of the operator's labor and of other unpaid labor as well as that of labor paid for in cash.

On cost-account farms on which the conditions were similar to those in Steuben County, the cost of horse labor averaged approximately 15 cents per hour. This rate was used in calculating the cost of production.

The average time required per acre for growing and marketing the crop was 79.6 man hours and 85 horse hours. The average cost per acre for man and horse labor was $26.68. These figures are shown in table 9:

TABLE 9. Hours and Cost of Labor in Growing and Marketing Potatoes, 355 Farms, 5227.1 Acres, Steuben County, 1912

| | Total hours | Total cost | Average hours per acre | Average cost per acre |
|---|---|---|---|---|
| Man labor | 416,099 | $72,817 | 79.6 | $13.93 |
| Horse labor | 444,494 | 66,671 | 85.0 | 12.75 |
| Total cost | ..... | $139,488 | ..... | $26.68 |

*Distribution of labor by operations.*— The average farmer used 9.4 hours of man labor and 22.7 hours of horse labor to prepare an acre for potatoes. This included plowing 1 time, harrowing 3 times, and rolling 0.4 time. Planting included hauling fertilizer and seed, cutting seed, marking rows, planting, and covering. Twenty-five per cent of the area in potatoes was planted with a machine planter. Cultivation of the crop required an average of 14.3 hours of man labor and 19.8 hours of horse labor. This included recovering 0.7 time, weeding and planking 1.1 times, cultivating 4 times, hilling or shovel-plowing 1.9 times, and hoeing 0.1 time. Potatoes were sprayed an average of 0.6 time. A large part of this work

was done with hand sprayers, using insecticide, and hence the proportion of man labor to horse labor is high. Harvesting included digging and picking up the crop and hauling to storage, also such operations as cultivating immediately before digging, and harrowing after digging. Seventy-five per cent of the total area in potatoes was dug with a machine digger.

The average time required to market an acre of potatoes, or 107.3 bushels, was 14.7 man hours and 16.5 horse hours. The labor of sorting was 6.5 man hours per acre, or 6.1 man hours per 100 bushels marketed. This was unusually high because of a severe attack of late blight in 1912 and a consequent rot in storage. The average time required per acre for hauling an average distance of 3.3 miles to market was 8.2 man hours and 16.5 horse hours.

The data are given in table 10:

TABLE 10. DISTRIBUTION OF LABOR BY OPERATIONS, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Number of times over the ground | Total hours of labor | | Average hours of labor per acre | |
|---|---|---|---|---|---|
| | | Man | Horse | Man | Horse |
| Plowing | 1.0 | 30,401 | 71,187 | 5.8 | 13.6 |
| Fitting | 3.4 | 18,684 | 47,655 | 3.6 | 9.1 |
| Planting | ..... | 58,927 | 37,748 | 11.3 | 7.2 |
| Recovering | 0.7 | 7,034 | 14,050 | 1.4 | 2.7 |
| Weeding and planking | 1.1 | 4,249 | 5,130 | 0.8 | 1.0 |
| Cultivating | 4.0 | 41,490 | 50,892 | 7.9 | 9.7 |
| Hilling | 1.9 | 20,598 | 33,415 | 3.9 | 6.4 |
| Hoeing | 0.1 | 1,824 | ..... | 0.3 | ..... |
| Spraying | 0.6 | 4,954 | 2,419 | 1.0 | 0.5 |
| Harvesting | ..... | 151,029 | 95,948 | 28.9 | 18.4 |
| Sorting | ..... | 34,005 | ..... | 6.5 | ..... |
| Hauling to market | ..... | 42,904 | 86,050 | 8.2 | 16.5 |
| Total hours | ..... | 416,099 | 444,494 | 79.6 | 85.0 |

*Probable error in hours of labor.*— The probable error in man hours per acre is ±0.16. Hence the man labor requirement per acre is 79.6±0.16 hours.

*Use of equipment*

The potato crop uses some equipment that is high in its initial cost and has a high rate of depreciation. However, the high cost of such equipment as diggers and sprayers should be averaged with the low cost of such equipment as wagons, plows, harrows, and cultivators. There is no reason for believing that the average cost of equipment per horse hour on potatoes is higher than the average cost of equipment per horse hour on the farm as a whole. On the cost-account farms the use of equipment averaged from 4 to 6 cents per horse hour. Five cents per horse hour seemed to be a fair charge for equipment in this region. On each record this charge was calculated to the nearest dollar. The total cost for use of equipment was $22,223, or $4.25 per acre.

*Miscellaneous items*

All other charges, including that for crates to maintain the supply on hand, small equipment not used with horses (as hooks and hand sprayers), land plaster for cut seed, and materials for treating seed, amounted to $1297, or 25 cents per acre. The items and their cost are given in table 11:

TABLE 11. Miscellaneous Items, 355 Farms, 5227.1 Acres, Steuben County, 1912

| | Total cost | Average cost per acre |
|---|---|---|
| Crates | $1,140 | $0.22 |
| Hooks and sprayers | 111 | 0.02 |
| Dust for cut seed | 45 | 0.01 |
| Formalin | 1 | ..... |
| | $1,297 | $0.25 |

*Returns from the potato crop*

The average yield of potatoes in Steuben County in 1912 was 121.7 bushels per acre. This does not include an average loss of 15 bushels per acre due to rot and to shrinkage in storage, but includes only the potatoes actually disposed of. The average value of potatoes per acre was $53.59. The data on yield and value are given in table 12:

TABLE 12. YIELD AND VALUE OF POTATOES PRODUCED ON 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Bushels | Value | Average price per bushel |
|---|---|---|---|
| Sold | 561,044 | $247,472 | $0.44 |
| Seed for 1913 | 50,879 | 24,888 | 0.49 |
| Fed to stock | 9,189 | 1,329 | 0.14 |
| Home use | 15,002 | 6,437 | 0.43 |
| Total | 636,114 | $280,126 | $0.44 |

*Summary of costs, returns, and profits*

The average cost per acre of growing and marketing was $51.13, or 42 cents per bushel. The average price received per bushel was 44 cents. The average cost per acre of growing without marketing was $45.26, or 37 cents per bushel. The average cost per acre of marketing was $5.87, or 5½ cents per bushel marketed. The summary of costs, returns, and profits is given in table 13:

TABLE 13. SUMMARY OF COSTS, RETURNS, AND PROFITS OF GROWING AND MARKETING POTATOES, 355 FARMS, 5227.1 ACRES, STEUBEN COUNTY, 1912

| | Total | Average per acre | Per cent of total cost |
|---|---|---|---|
| COSTS | | | |
| Seed | $49,539 | $ 9.48 | 18.5 |
| Manure | 25,064 | 4.80 | 9.4 |
| Fertilizer | 8,675 | 1.66 | 3.2 |
| Spray materials | 1,032 | 0.20 | 0.4 |
| Land rental | 15,681 | 3.00 | 5.9 |
| Use of buildings | 4,226 | 0.81 | 1.6 |
| Man labor | 72,817 | 13.93 | 27.3 |
| Horse labor | 66,671 | 12.75 | 24.9 |
| Use of equipment | 22,223 | 4.25 | 8.3 |
| Miscellaneous items | 1,297 | 0.25 | 0.5 |
| Cost of growing and marketing | $267,225 | $51.13 | 100.0 |
| Cost of growing without marketing | 236,556 | 45.26 | |
| Cost of marketing | 30,669 | 5.87 | |
| RETURNS | | | |
| Potatoes, 636,114 bushels | $280,126 | $53.59 | |
| PROFITS | $12,901 | $2.46 | |

*Probable error in total cost.*— The probable error in the cost per acre of growing and marketing potatoes is ±0.086, making this cost $51.13 ±0.086. The probable error in the cost per bushel of growing and marketing is ±0.0001, making this item $0.42 ±0.0001.

## COST OF POTATO PRODUCTION ON 300 FARMS IN CLINTON AND FRANKLIN COUNTIES, 1913 [2]

### *Description of the region*

The topography of the area studied in Clinton and Franklin Counties varies from gently rolling to hilly. The general slope is to the north and northeast. Owing to the rough, stony character of the soil, on many farms the fields are limited to small, irregular areas. The elevation of a large proportion of the farms studied is between 800 and 1500 feet.

The soils on the farms studied are largely of the Coloma series. Fine sandy loam is the predominating type in the northern part of the area, and stony fine sandy loam in the southern part. The soil is well drained The principal crops were potatoes, oats, and hay. The yield of potatoes was 179 bushels per acre, of oats 44.5 bushels per acre, and of hay 1 ton per acre.

The length of the growing season varies from 120 to 140 days, which is about the same as the growing season in Steuben County and from 30 to 80 days shorter than that on Long Island. The average rainfall for April to August inclusive varies from 16 to 18 inches. The rainfall for 1913 at Dannemora was 11 inches for this period.

The average farm raised 72 acres of crops. The average acreage in potatoes was 7.2 acres. The average size of field in potatoes was less than this. The following crops were grown in 1913: potatoes on 10 per cent of the crop area, hay on 61 per cent, oats on 20 per cent, and corn on 6 per cent.

### *Seed*

An average of 12 bushels of seed was used per acre (table 14). The average cost of seed per bushel was 57 cents, and the average cost per acre was $6.79.

[2] The source of the data here given on potato production in Clinton and Franklin Counties is a thesis by W. M. Peacock, entitled *Factors Influencing the Cost of Potato Production in Clinton and Franklin Counties, New York*, in the Cornell University Library.

TABLE. 14. QUANTITY AND COST OF SEED, 300 FARMS, 2160 ACRES, CLINTON AND FRANKLIN COUNTIES, 1913

| | Total | Average per acre |
|---|---|---|
| Bushels used | 25,959 | 12 |
| Cost | $14,669 | $6.79 |

*Manure*

Because the soil of this area is mainly a fine sandy loam, the residual effects of manure are less than on a heavier soil. It was estimated, therefore, that potatoes should pay for 50 per cent of the manure applied directly to the crop and 30 per cent of the manure applied to the preceding crop. On this basis the 1913 crop grown on 1406.5 acres should pay for 9242 tons of manure, or an average of 6.6 tons per acre. The quantity of manure used, and its cost, are shown in table 15:

TABLE 15. QUANTITY AND COST OF MANURE USED, 300 FARMS, 2160 ACRES, CLINTON AND FRANKLIN COUNTIES, 1913

| | Total | Average per acre for all farms |
|---|---|---|
| Tons used by potatoes | 9,242 | 4.3 |
| Cost | $15,576 | $7.21 |

*Fertilizer*

Fertilizer was applied on 1468 acres of potatoes at an average rate of 599 pounds per acre. The average price of fertilizer at the railway station was $28.34 per ton. The data for this item are given in table 16:

TABLE 16. QUANTITY AND COST OF FERTILIZER USED, 300 FARMS, 2160 ACRES, CLINTON AND FRANKLIN COUNTIES, 1913

| | Total | Average per acre for all farms |
|---|---|---|
| Pounds used | 879,400 | 407 |
| Cost | $12,460 | $5.77 |

*Spray materials*

Potatoes were sprayed with arsenical poisons on 203 of the 300 farms. Only three farmers sprayed with bordeaux. Late blight is seldom prevalent in this region, and when present it is not very destructive. It is doubtful whether it would pay the farmers of Clinton and Franklin Counties to spray with bordeaux. The total cost of spray materials was $475, or an average cost of 22 cents per acre for all farms.

*Land rental*

The average value of the crop land, without buildings, on the farms studied in Clinton and Franklin Counties was almost exactly the same as in Steuben County. Consequently the same charge of $3 per acre was made for land rental. As in Steuben County, 5 per cent was allowed for interest on investment and 1 per cent for taxes and upkeep. The total cost for use of land for the 2160 acres was $6480.

*Use of buildings*

Potatoes not sold in the fall were usually stored in cellars under farm buildings. Many cellars had either a double stone wall or an outer stone wall with an inner wooden casing and a dead-air space between. Eighty-eight per cent of the marketed potatoes, or 271,060 bushels, were stored. In addition to these, 77,449 bushels saved for seed and for home use were stored. The use of buildings was charged at 8 per cent on the value of the part of the building used for storage. This was to cover interest on investment, taxes, and upkeep expenses. It was calculated that the use of buildings cost $4496. Since 348,509 bushels were stored, the average cost per bushel stored was 1.3 cents. The average cost for use of buildings was $2.08 per acre.

*Labor*

The same charge was made for man and horse labor as in Steuben County. Approximately the same wages were paid for man labor in Clinton and Franklin Counties as in Steuben County, and the factors affecting the cost of horse labor were similar.

Labor was used much less efficiently in Clinton and Franklin Counties than in Steuben County. The total hours of growing and marketing per acre were 122.6 man hours and 102.8 horse hours. This was 43 man hours and 17.8 horse hours per acre more than was required in Steuben

County. Thus a yield per acre 47 per cent higher than the yield on the farms in Steuben County required more labor in picking up and marketing. A large part of the difference in labor requirement, however, was due to the small, irregular fields, which made very efficient use of labor difficult. Very little labor-saving machinery was used because of the small, irregular fields and the presence of stones on many farms in sufficient quantity to seriously interfere with the use of machinery. A comparison of the ratio of man labor to horse labor in Steuben County and in Clinton and Franklin Counties shows that much less work was done with three-horse teams in the latter area. Also, more time was required for many of the operations. Plowing required 5.8 man hours and 13.6 horse hours per acre on the farms in Steuben County, and 8.3 man hours and 17.1 horse hours on the farms in Clinton and Franklin Counties. In fitting the ground, 3.6 man hours and 9.1 horse hours were required on the farms in Steuben County, and 6.7 man hours and 15.4 horse hours on the farms in Clinton and Franklin Counties.

Of the total labor per acre of 122.6 man hours and 102.8 horse hours, 12.2 man hours and 24.3 horse hours were required to haul the crop to market. The average cost per acre of man and horse labor in growing and marketing potatoes was $36.88, as shown in table 17:

TABLE 17. HOURS AND COST OF LABOR IN GROWING AND MARKETING POTATOES, 300 FARMS, 2160 ACRES, CLINTON AND FRANKLIN COUNTIES, 1913

| | Total hours | Total cost | Average hours per acre | Average cost per acre |
|---|---|---|---|---|
| Man labor | 264,758 | $46,333 | 122.6 | $21.45 |
| Horse labor | 222,142 | 33,321 | 102.8 | 15.43 |
| Total cost | ..... | $79,654 | ..... | $36.88 |

*Use of equipment*

The same charge was made for use of equipment as in Steuben County, 5 cents per horse hour. Altho less labor-saving machinery was used than in Steuben County, it is probable that the harder wear on all the machinery, in the stony, sandy soil, more than offset the saving in sprayers and diggers. The total cost for use of equipment was $11,107, or an average of $5.14 per acre.

*Miscellaneous items*

The miscellaneous items, including baskets, crates, bags, and material for treating seed, amounted to $741, or an average of 34 cents per acre.

*Returns from the potato crop*

Twenty per cent of the crop raised in Clinton and Franklin Counties was consumed on the farm or saved for seed. The remaining 80 per cent was sold. The average yield per acre was 179.3 bushels (table 18). The average value was 58 cents per bushel.

TABLE 18. Yield and Value of Potatoes Produced on 300 Farms, 2160 Acres, Clinton and Franklin Counties, 1913

| | Total | Average per acre |
|---|---|---|
| Bushels | 387,288 | 179.3 |
| Value | $224,046 | $103.72 |

*Summary of costs, returns, and profits*

The average cost per acre of growing and marketing was $67.43, or 38 cents per bushel. The average price received per bushel was 58 cents.

TABLE 19. Summary of Costs, Returns, and Profits of Growing and Marketing Potatoes, 300 Farms, 2160 Acres, Clinton and Franklin Counties, 1913

| | Total | Average per acre | Per cent of total cost |
|---|---|---|---|
| COSTS | | | |
| Seed | $14,669 | $ 6.79 | 10.1 |
| Manure | 15,576 | 7.21 | 10.7 |
| Fertilizer | 12,460 | 5.77 | 8.6 |
| Spray materials | 475 | 0.22 | 0.3 |
| Land rental | 6,480 | 3.00 | 4.4 |
| Use of buildings | 4,496 | 2.08 | 3.1 |
| Man labor | 46,333 | 21.45 | 31.8 |
| Horse labor | 33,321 | 15.43 | 22.9 |
| Use of equipment | 11,107 | 5.14 | 7.6 |
| Miscellaneous items | 741 | 0.34 | 0.5 |
| Cost of growing and marketing | $145,658 | $67.43 | 100.0 |
| RETURNS | | | |
| Potatoes, 387,288 bushels | $224,046 | $103.72 | |
| PROFITS | $78,388 | $36.29 | |

The average cost of hauling to market was 4.9 cents per bushel marketed. The summary of costs, returns, and profits is given in table 19.

## COST OF POTATO PRODUCTION, 26 RECORDS ON 20 COST-ACCOUNT FARMS, 1913, 1914, AND 1915

The cost-account data were composed of records of 26 crops of potatoes on 20 farms, for 1913, 1914, and 1915. Of these records, nine were for 1913, nine for 1914, and eight for 1915. The farms were located in Allegany, Cayuga, Chemung, Erie, Livingston, Monroe, Ontario, Steuben, Tompkins, and Wyoming Counties. The average area in crops on these farms was 113.8 acres, or 40 per cent greater than the average of the farms studied in Steuben County. The average area in potatoes was 13 acres. As the complete data for marketing the 1915 crop were not available, only the cost of growing is here considered.

### *Seed*

An average of 14.7 bushels of seed per acre was used, at a cost of 47 cents per bushel. The total cost of the seed, and the average cost per acre, are given in table 20:

TABLE 20. QUANTITY AND COST OF SEED, 26 CROPS, 20 FARMS, 338.5 ACRES, COST ACCOUNTS, 1913, 1914, AND 1915

| | Total | Average per acre |
|---|---|---|
| Bushels used | 4,966.8 | 14.7 |
| Cost | $2,338.31 | $6.91 |

### *Manure*

Manure was charged on the basis of 40, 30, 20, and 10 per cent to the first, second, third, and fourth crops, respectively. All but one crop of potatoes received some manure. The total cost of the manure apportioned to potatoes was $1956.65, or an average of $5.78 per acre.

### *Fertilizer*

Twenty-two farms used commercial fertilizer on 303.7 acres. The average rate of application per acre for those using it was 511 pounds.

The average cost at the railroad station of the fertilizer used was $24.36 per ton. The data are given in table 21:

TABLE 21. Quantity and Cost of Fertilizer Used, 26 Crops, 20 Farms, 338.5 Acres, Cost Accounts, 1913, 1914, and 1915

| | Total | Average per acre for all farms |
|---|---|---|
| Pounds used | 155,115 | 458 |
| Cost | $1,889.95 | $5.58 |

*Spray materials*

Potatoes were sprayed on 16 of the 26 farms. Bordeaux was used on 152.5 acres on 8 farms. The average cost for fungicides and insecticides on these 8 farms was $1.92 per acre. Data on the cost of the spray materials used are given in table 22:

TABLE 22. Cost of Spray Materials Used, 26 Crops, 20 Farms, 338.5 Acres, Cost Accounts, 1913, 1914, and 1915

| | |
|---|---|
| Total cost | $312.80 |
| Average cost per acre for all farms | 0.92 |

*Land rental*

The average value of the crop land for potatoes was $74.50 per acre. A rental charge of 5 per cent of the value for interest and 1 per cent for taxes and upkeep was made. The value of the crop land in potatoes varied from $20 to $133.33 per acre, with a corresponding range in rental from $1.20 to $8 per acre. The total cost for land rental was $1511.51, or $4.47 per acre.

*Use of buildings*

Ninety-two per cent of the total crop was stored. Most of the potatoes were stored in the cellars of farmhouses. The average cost for use of buildings was a small fraction over one cent per bushel stored. This represents a rental charge of 8 per cent on the value of the part of the building used for storage. The data are given in table 23:

TABLE 23. COST FOR USE OF BUILDINGS, 26 CROPS, 20 FARMS, 338.5 ACRES, COST ACCOUNTS, 1913, 1914, AND 1915

| | Total | Average per acre |
|---|---|---|
| Bushels stored | 39,024 | 115.3 |
| Cost for use of buildings | $400.10 | $1.18 |

*Labor*

The average time required to grow the crop was 73.1 man hours and 74.5 horse hours, as shown in table 24. Since a part of the crop was inventoried on many farms when the accounts were closed, the labor of marketing was not complete and is not here considered. The average cost of man labor was 18.6 cents per hour, and of horse labor 14.9 cents per hour. These rates were determined by cost-account methods, but the time of the operator is included at the wages paid to hired labor, which is below its real value.

TABLE 24. HOURS AND COST OF LABOR IN GROWING POTATOES, 26 CROPS, 20 FARMS, 338.5 ACRES, COST ACCOUNTS, 1913, 1914, AND 1915

| | Total hours | Total cost | Average hours per acre | Average cost per acre |
|---|---|---|---|---|
| Man labor | 24,753 | $4,597.80 | 73.1 | $13.58 |
| Horse labor | 25,204 | 3,745.12 | 74.5 | 11.06 |
| Total cost | ..... | $8,342.92 | ..... | $24.64 |

*Distribution of labor by operations.*— In 15 of the 26 cost-account records, labor was recorded in such a way that its distribution could be studied. The preparation of the ground required 9.8 man hours and 25.7 horse hours per acre (table 25). This included plowing, harrowing, and rolling before planting. Planting required 13.2 man hours and 8.7 horse hours per acre. This included hauling fertilizer and seed, cutting seed, marking, planting, covering, and rolling after planting.

The cultural operations consisted of recovering, weeding and planking, cultivating, and hilling, and were usually performed in the order given.

TABLE 25. Distribution of Labor by Operations, 15 Crops, 183.6 Acres, Cost Accounts, 1913, 1914, and 1915

| | Total hours of labor | | Average hours of labor per acre | |
|---|---|---|---|---|
| | Man | Horse | Man | Horse |
| Plowing | 1,152.3 | 2,971 | 6.3 | 16.2 |
| Fitting | 658.5 | 1,736.5 | 3.5 | 9.5 |
| Planting | 2,423.5 | 1,590 | 13.2 | 8.7 |
| Recovering | 65.5 | 131 | 0.4 | 0.7 |
| Weeding and planking | 106.6 | 171.3 | 0.6 | 0.9 |
| Cultivating | 1,396 | 1,947 | 7.6 | 10.6 |
| Hilling | 277 | 455.5 | 1.5 | 2.5 |
| Spraying | 92 | 105 | 0.5 | 0.6 |
| Digging | 5.913 | 3,893.5 | 32.2 | 21.2 |
| All else | 749 | 299.8 | 4.1 | 1.6 |
| Total hours | 12,833.4 | 13,300.6 | 69.9 | 72.4 |

These four cultural operations required 10.1 man hours and 14.7 horse hours per acre. Since in the case of only 2 of these 15 records spraying machinery was used, the average time per acre for all the farms is low — 0.5 man hour and 0.6 horse hour. Digging required 32.2 man hours and 21.2 horse hours per acre. The work listed as "All else" included sorting seed, treating seed, spraying for bug control with hand sprayers, and like operations.

*Distribution of labor by 10-day periods.*— In the 15 accounts studied for distribution of labor, 36.4 per cent of the man labor and 44.2 per cent of the horse labor was done between May 21 and July 20, and 44.6 of the man labor and 28 per cent of the horse labor was done between October 1 and November 20. The work in the earlier period conflicts more seriously with farm operations than that in the later period, because more horse labor is required and because the heavy demand on man labor in the later period can be overcome by employing transient labor, which is not so available in the earlier season. The labor on potatoes between May 21 and June 20 is likely to conflict with work on cabbage, beans, and corn. The labor on potatoes between June 21 and July 20 conflicts with work on alfalfa and on timothy and clover hay.

The data are given in table 26, and are shown graphically in figures 82 and 83.

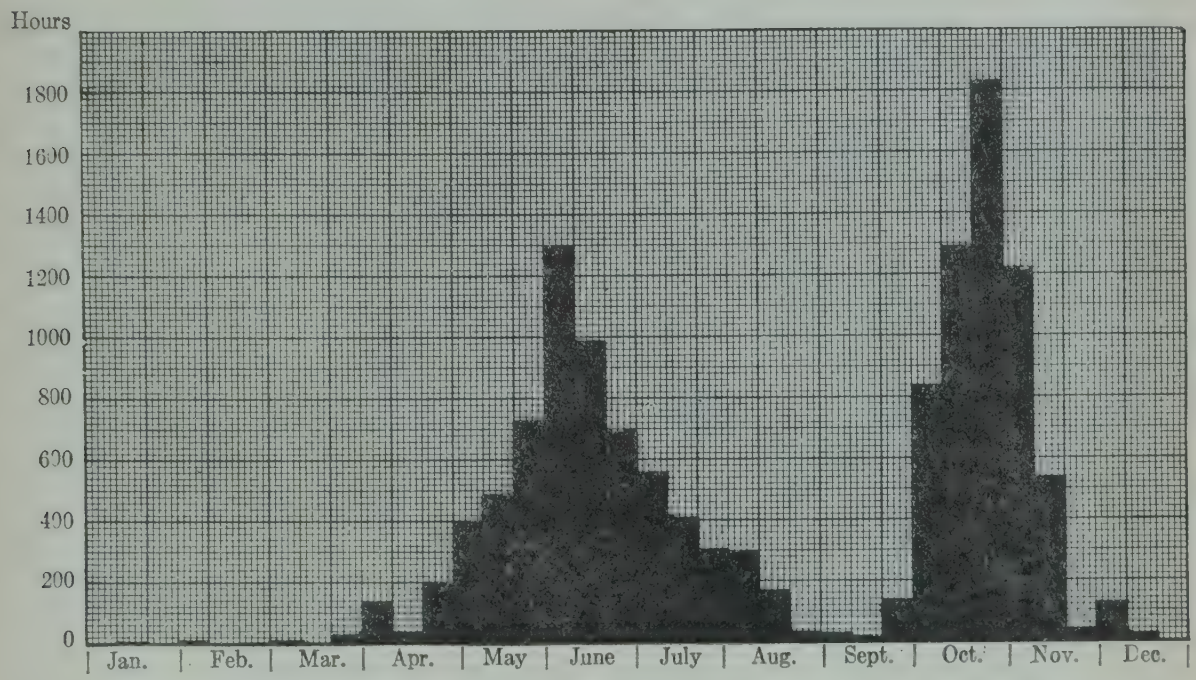


FIG. 82. DISTRIBUTION OF MAN LABOR ON POTATOES BY 10-DAY PERIODS, 15 CROPS, 183.6 ACRES, COST ACCOUNTS

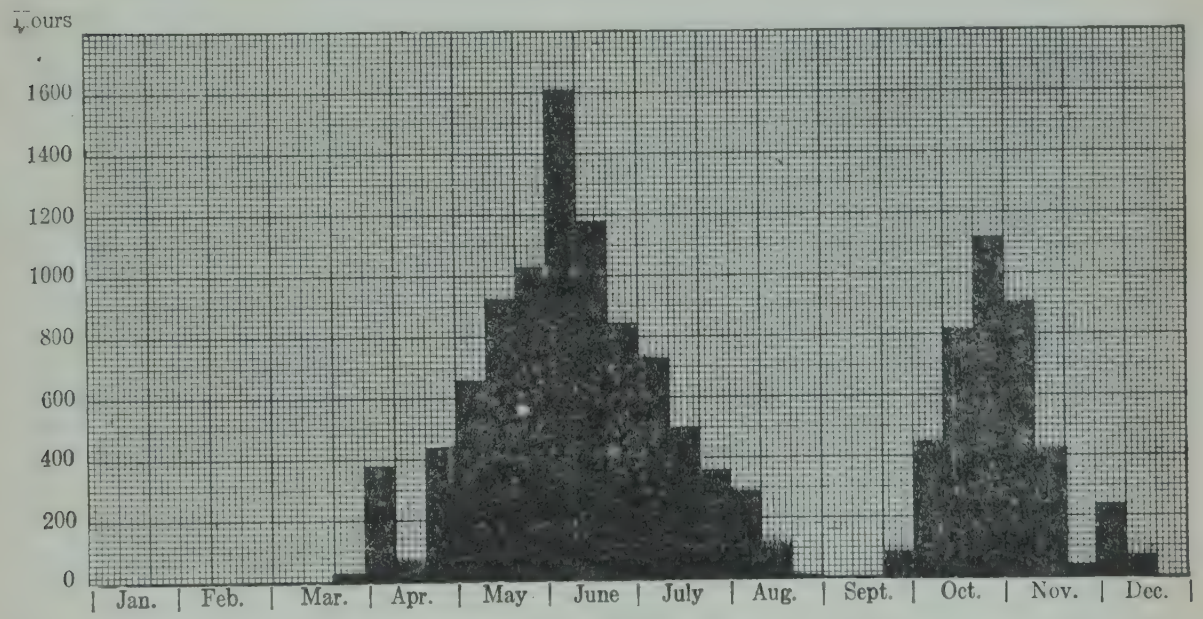


FIG. 83. DISTRIBUTION OF HORSE LABOR ON POTATOES BY 10-DAY PERIODS, 15 CROPS, 183.6 ACRES, COST ACCOUNTS

*Use of equipment*

The average cost per horse hour for equipment used on potatoes was 4.4 cents. The total cost for use of equipment was $1112.14, or an average of $3.29 per acre.

*Miscellaneous items*

Miscellaneous items charged on the cost-account farms included the following: materials to treat seed, $1.10; dues to Potato Growers' Association, $1; potato-show expenses, 39 cents; postage, 15 cents. The total cost for miscellaneous items was $2.64, or less than one cent per acre.

*Marketing cost*

The cost of man and horse labor and the use of equipment to market a part of the crop on the cost-account farms amounted to $1378.99.

*Returns from the potato crop*

When the accounts were closed on the cost-account farms, the portion of the potato crop that had not been sold was inventoried at farm value. The average number of bushels per acre disposed of or inventoried was 125.6, worth $64.78 (table 27). The average value was 52 cents per bushel.

TABLE 27. Yield and Value of Potatoes, 26 Crops, 20 Farms, 338.5 Acres, Cost Accounts, 1913, 1914, and 1915

| | Total | Average per acre |
|---|---|---|
| Bushels | 42,519 | 125.6 |
| Value | $21,927.15 | $64.78 |

*Summary of costs, returns, and profits*

The average cost of growing potatoes was $52.78 per acre. This does not include the cost of marketing, which for the potatoes marketed averaged $4.07 per acre. The average profit was $7.92 per acre. Thirteen of the 26 records showed a loss. The summary of costs, returns, and profits is given in table 28:

TABLE 28. SUMMARY OF COSTS, RETURNS, AND PROFITS OF GROWING POTATOES, 26 CROPS, 20 FARMS, 338.5 ACRES, COST ACCOUNTS, 1913, 1914, AND 1915

| | Total | Average per acre | Per cent of total cost |
|---|---|---|---|
| COSTS | | | |
| Seed | $2,338.31 | $ 6.91 | 13.1 |
| Manure | 1,956.65 | 5.78 | 10.9 |
| Fertilizer | 1,889.95 | 5.58 | 10.6 |
| Spray materials | 312.80 | 0.92 | 1.8 |
| Land rental | 1,511.51 | 4.47 | 8.5 |
| Use of buildings | 400.10 | 1.18 | 2.2 |
| Man labor | 4,597.80 | 13.58 | 25.7 |
| Horse labor | 3,745.12 | 11.06 | 21.0 |
| Use of equipment | 1,112.14 | 3.29 | 6.2 |
| Miscellaneous items | 2.64 | 0.01 | 0.0 |
| Cost of growing without marketing | $17,867.02 | $52.78 | 100.0 |
| Cost of marketing a part of the crop | 1,378.99 | | |
| RETURNS | | | |
| Potatoes, 42,519 bushels | $21,927.15 | $64.78 | |
| PROFITS | $2,681.14 | $7.92 | |

## COST OF POTATO PRODUCTION ON 161 FARMS IN SUFFOLK COUNTY, 1912

### *Description of the region*

The region studied in Suffolk County is located in the eastern part. It is a level coastal plain area, from 10 to 100 feet above sea level.

The soils in this region have not been definitely classified. Probably the predominating soil is Sassafras sandy loam. It is a well-drained, very easily tilled soil. The normal length of the growing season varies from 190 to 200 days, which is from 50 to 80 days longer than in Steuben, Clinton, and Franklin Counties. The normal rainfall for March to July inclusive, the periods during which potatoes would be most affected, is approximately 18 inches. On the farms studied, the smallest acreage in potatoes was 5 acres and the largest was 72 acres. The average was 19.6 acres per farm.

### *Seed*

As shown in table 29, an average of 11.9 bushels of seed per acre, worth $14.70, was planted. The average value of the seed per bushel was $1.23. Three farmers used less than 9 bushels of seed per acre, and 15 farmers used more than 14 bushels per acre.

TABLE 29. QUANTITY AND COST OF SEED, 161 FARMS, 3149.7 ACRES, SUFFOLK COUNTY, 1912

| | Total | Average per acre |
|---|---|---|
| Bushels used | 37,531.1 | 11.9 |
| Cost | $46,306 | $14.70 |

FIG. 84. A TYPICAL FIELD OF POTATOES IN SUFFOLK COUNTY
Beyond the low sand hill is the Atlantic Ocean

### *Manure*

Stable manure was applied to potatoes on 22 of the 161 farms in 1912. On only 7 farms was it applied to the entire acreage of potatoes. A total of 160.9 acres was manured, at an average rate of 14.1 tons per acre. The quantity and the cost of the manure used are given in table 30. The cost of the manure included its value at the price paid for the quantity bought and the farmer's estimate of the value of the manure made on the

farm, plus an estimated cost of 50 cents per ton for application. It was estimated that potatoes should pay for 50 per cent of the cost of manure applied to the crop.

TABLE 30. QUANTITY AND COST OF MANURE USED, 161 FARMS, 3149.7 ACRES, SUFFOLK COUNTY, 1912

| | Total | Average per acre for all farms |
|---|---|---|
| Tons used by potatoes | 1,132 | 0.36 |
| Cost | $2,776 | $0.88 |

A few farmers used manure on the crop preceding potatoes, and a few grew a cover crop to plow under for potatoes. The residual manure and the green manure were not included in the manure costs. Altho the amounts would have been small, they should have been included. The error is corrected largely by a higher rental for the potato land on these farms.

*Fertilizer*

Fertilizer was applied to potatoes on every farm studied in Suffolk County. A total of 5,796,700 pounds was used, or an average of 1840 pounds per acre (table 31). The amount applied per acre varied from 1250 pounds to 3000 pounds. Less than 1500 pounds per acre was applied on 5 farms, and more than 2000 pounds per acre was applied on 17 farms. The average cost of the fertilizer at the railway station was $30.44 per ton.

TABLE 31. QUANTITY AND COST OF FERTILIZER USED, 161 FARMS, 3149.7 ACRES, SUFFOLK COUNTY, 1912

| | Total | Average per acre |
|---|---|---|
| Pounds used | 5,796,700 | 1,840 |
| Cost | $88,220 | $28.01 |

*Spray materials*

Potatoes were sprayed with bordeaux on 1007.7 acres on 47 farms. These farms were distributed fairly equally over the region. Every farm used arsenical poison for potato bugs. Traction sprayers were used on 137

farms, traction dusters (fig. 85) on 31 farms, hand dusters on 22 farms, and hand-pump sprayers on 1 farm. The average cost for fungicide materials

FIG. 85. TRACTION DUSTER IN USE ON LONG ISLAND

per acre on the farms using them was $1.95. The average cost of insecticide materials per acre for all farms was 68 cents, as shown in table 32:

TABLE 32. COST OF SPRAY MATERIALS USED, 161 FARMS, 3149.7 ACRES, SUFFOLK COUNTY, 1912

| | Total cost | Average cost per acre for all farms |
|---|---|---|
| Fungicides | $1,966 | $0.62 |
| Insecticides | 2,138 | 0.68 |
| Total cost of spray materials | $4,104 | $1.30 |

*Land rental*

The charge for land rental was based on the farmers' estimates of the rental value of the crop land without buildings. As considerable land was rented in Suffolk County, this was the best method of determining the land rental. The total rental for 3149.7 acres of potato land was $40,342, or an average of $12.81 per acre.

*Use of buildings*

The cost of use of buildings for storing potatoes was estimated by each farmer. As but few potatoes were stored, this cost was low, the total being $1574, or 50 cents per acre.

*Labor*

An average of 77.4 man hours and 68.2 horse hours was required to grow and market the crop (table 33). The cost of labor was estimated in the same way as in Steuben County and the same rates were used — 17½ cents per hour for man labor and 15 cents per hour for horse labor.

TABLE 33. HOURS AND COST OF LABOR IN GROWING AND MARKETING POTATOES, 161 FARMS, 3149.7 ACRES, SUFFOLK COUNTY, 1912

| | Total hours | Total cost | Average hours per acre | Average cost per acre |
|---|---|---|---|---|
| Man labor | 243,720 | $42,654 | 77.4 | $13.54 |
| Horse labor | 214,772 | 32,217 | 68.2 | 10.23 |
| Total | ..... | $74,871 | ..... | $23.77 |

*Distribution of labor by operations.*— Plowing, harrowing 1.7 times, and rolling 0.1 time took an average of 5.3 man hours and 11.8 horse hours per acre (table 34). Planting the crop required an average of 12.1 man hours and 8.9 horse hours per acre. This included: planting potatoes, an average of 3.5 man hours and 5.4 horse hours per acre; cutting seed, an average of 6.4 man hours per acre; sprouting and treating seed, an average of 0.1 man hour per acre; hauling fertilizer, and drilling when fertilizer was applied ahead of the planter, an average of 2.1 man hours and 3.5 horse hours per acre.

The cultural operations consisted of weeding and harrowing, cultivating, hilling, and hoeing. The farmers in Suffolk County cultivated and hoed the crop more than those in any of the other areas studied. They did no recovering and but little hilling.

Spraying required an average of 2.4 man hours and 3.1 horse hours per acre.

Harvesting the potato crop required 25.1 man hours and 15.2 horse hours. Marketing required 8.9 man hours and 10.3 horse hours. This included the labor of sorting and hauling to the shipping station.

TABLE 34. Distribution of Labor by Operations, 161 Farms, 3149.7 Acres, Suffolk County, 1912

| | Number of times over the ground | Total hours of labor | | Average hours of labor per acre | |
|---|---|---|---|---|---|
| | | Man | Horse | Man | Horse |
| Plowing | ..... | 12,149 | 27,205 | 3.9 | 8.6 |
| Fitting | 1.8 | 4,414 | 9,961 | 1.4 | 3.2 |
| Planting | ..... | 37,988 | 28,153 | 12.1 | 8.9 |
| Weeding and harrowing | ..... | 7,342 | 8,572 | 2.3 | 2.7 |
| Cultivating | ..... | 30,345 | 48,131 | 9.6 | 15.3 |
| Hilling | ..... | 1,874 | 2,418 | 0.6 | 0.8 |
| Hoeing | ..... | 35,275 | ..... | 11.2 | ..... |
| Spraying | 3.2 | 7,460 | 9,848 | 2.4 | 3.1 |
| Harvesting | ..... | 78,927 | 47,973 | 25.1 | 15.2 |
| Sorting | ..... | 10,632 | ..... | 3.4 | ..... |
| Marketing | ..... | 17,314 | 32,511 | 5.5 | 10.3 |
| Total hours | ..... | 243,720 | 214,772 | 77.4 | 68.2 |

*Probable error in hours of labor.*— The probable error in hours of man labor per acre in Suffolk County is ±0.21, making the man labor requirement per acre 77.4±0.21 hours. The probable error of the horse hours per acre is ±0.22, making the horse labor requirement per acre 68.2±0.22 hours.

### *Use of equipment*

The use of equipment was estimated to be 5 cents per horse hour, which was the rate used in Steuben County and in Clinton and Franklin Counties. The total cost for use of equipment was $10,739, or $3.41 per acre.

*Miscellaneous items*

Miscellaneous items included: baskets, $182; dust for cut seed, $243; materials for treating seed, $3; other miscellaneous items, $12. The total cost for miscellaneous items was $440, or an average of 14 cents per acre.

*Returns from the potato crop*

A total of 496,255 bushels, or an average of 157.6 bushels per acre, was harvested. The crop was worth $350,181, or an average of $111.18 per acre. Of the total amount harvested, 17,062 bushels were used for seed, 6727 bushels were used in the house, and 480 bushels were fed to stock. The average value of the crop was 71 cents per bushel.

*Summary of costs, returns, and profits*

The average farmer in Suffolk County grew and marketed potatoes at a cost of 54 cents per bushel. The average cost of growing the potatoes was 52 cents per bushel. The summary of costs, returns, and profits is given in table 35:

TABLE 35. Summary of Costs, Returns, and Profits of Growing and Marketing Potatoes, 161 Farms, 3149.7 Acres, Suffolk County, 1912

| | Total | Average per acre | Per cent of total cost |
|---|---|---|---|
| COSTS | | | |
| Seed | $46,306 | $14.70 | 17.2 |
| Manure | 2,776 | 0.88 | 1.0 |
| Fertilizer | 88,220 | 28.01 | 32.8 |
| Spray materials | 4,104 | 1.30 | 1.5 |
| Land rental | 40,342 | 12.81 | 15.0 |
| Use of buildings | 1,574 | 0.50 | 0.6 |
| Man labor | 42,654 | 13.54 | 15.8 |
| Horse labor | 32,217 | 10.23 | 11.9 |
| Use of equipment | 10,739 | 3.41 | 4.0 |
| Miscellaneous items | 440 | 0.14 | 0.2 |
| Cost of growing and marketing | $269,372 | $85.52 | 100.0 |
| Cost of growing without marketing | 257,979 | 81.91 | |
| Cost of marketing | 11,393 | 3.62 | |
| RETURNS | | | |
| Potatoes, 496,255 bushels | $350,181 | $111.18 | |
| PROFITS | $80,809 | $25.66 | |

*Probable error in total cost.*— The probable error in the cost per acre of growing and marketing potatoes in Suffolk County is ±0.141, making this cost $85.52±0.141. The probable error in the cost per bushel is ±0.00015, making this item $0.54±0.00015.

## COST OF POTATO PRODUCTION ON 41 FARMS IN NASSAU COUNTY, 1912

### *Description of the region*

The farms studied in Nassau County are located largely on the nearly level prairie land in the central part of the county. The elevation varies from 95 to 200 feet. The predominating soils are Hempstead loam, gravelly loam, and Sassafras gravelly loam. A few of the farms are on Plymouth sandy loam.

The normal length of the growing season is from 170 to 180 days. The normal rainfall from March to July inclusive is from 18 to 20 inches.

The smallest acreage in potatoes was 7.5 acres and the largest was 105 acres. The average was 35.8 acres.

### *Seed*

An average of 12.4 bushels of seed per acre, worth $15.28, was planted (table 36). The average cost of the seed per bushel was $1.23.

TABLE 36. QUANTITY AND COST OF SEED, 41 FARMS, 1466.3 ACRES, NASSAU COUNTY, 1912

| | Total | Average per acre |
|---|---|---|
| Bushels used | 18,202.5 | 12.4 |
| Cost | $22,398 | $15.28 |

### *Manure*

Stable manure was applied to potato land on 13 of the 41 farms. On only 2 farms was the entire acreage in potatoes manured. A total of 124.9 acres was manured, at an average rate of 13.4 tons per acre. The cost of manure was figured on the same basis as in Suffolk County. A total of 1668 tons was applied, of which potatoes should pay for 834 tons. A few farmers used green manure in the form of a cover crop or applied manure to the crop preceding potatoes in the rotation. These costs

were overlooked, as in Suffolk County. The quantity and the cost of the manure used by potatoes are given in table 37:

TABLE 37. Quantity and Cost of Manure Used, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Total | Average per acre for all farms |
|---|---|---|
| Tons used by potatoes | 834 | 0.57 |
| Cost | $2,461 | $1.68 |

*Fertilizer*

As in Suffolk County, every farmer used fertilizer on his potatoes. A total of 2,739,400 pounds was used, or an average of 1868 pounds per acre (table 38). The amount applied per acre varied from 1100 pounds to 2000 pounds. The average cost of the fertilizer at the railway station was $32.93 per ton.

TABLE 38. Quantity and Cost of Fertilizer Used, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Total | Average per acre |
|---|---|---|
| Pounds used | 2,739,400 | 1,868 |
| Cost | $45,101 | $30.76 |

On 11 farms the fertilizer was applied with a drill, and usually was spread in rows just ahead of the planter.

*Spray materials*

Potatoes were sprayed with bordeaux on 77.5 acres on 5 farms. Arsenical poisons for control of potato bugs were used on 38 farms. The average cost for fungicide materials per acre on farms spraying with bordeaux was $2.48. The average number of times sprayed with bordeaux was 5.3. The average cost per acre for insecticide materials, on the farms using them, was 72 cents. The total cost of spray materials, and the average cost for all farms, are given in table 39:

TABLE 39. Cost of Spray Materials Used, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Total cost | Average cost per acre for all farms |
|---|---|---|
| Fungicides | $ 192 | $0.13 |
| Insecticides | 1,028 | 0.70 |
| Total cost of spray materials | $1,220 | $0.83 |

Traction sprayers were used by 27 farmers, traction dusters by 11 farmers, and a hand duster by 1 farmer.

*Land rental*

The charge for land rental was based on the farmers' estimates of the rental value of the crop land without buildings. As the land in this

Fig. 86. A truck load of Nassau County potatoes ready for market

FIG. 87. A SCENE IN WALLABOUT MARKET, BROOKLYN

A large part of the potatoes raised in Nassau County are hauled on trucks to the Wallabout and Harlem markets, where the farmer sells directly to wholesale and retail merchants

section had a high real estate value and over half of the farms were rented, this was the best way of determining the land rental. The total rental for 1466.3 acres of potato land was $23,140, or $15.78 per acre.

*Use of buildings*

The cost for use of buildings in storing the potato crop was estimated by each farmer. As only a small proportion of the potatoes were stored, the cost was low. The total cost for use of buildings was $412, or 28 cents per acre.

*Labor*

As shown in table 40, an average of 107.2 man hours and 116.2 horse hours was required to grow and market an acre of potatoes in Nassau County. The average time required per acre for marketing was 28.1 man hours and 56.4 horse hours (table 41). This is high because all the potatoes were hauled to the New York or Brooklyn markets. The cost

per hour of labor was estimated in the same way as in Steuben County and the same rates were used — 17½ cents per hour for man labor and 15 cents per hour for horse labor.

TABLE 40. Hours and Cost of Labor in Growing and Marketing Potatoes, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Total hours | Total cost | Average hours per acre | Average cost per acre |
|---|---|---|---|---|
| Man labor | 157,222 | $27,510 | 107.2 | $18.76 |
| Horse labor | 170,353 | 25,552 | 116.2 | 17.43 |
| Total cost | ..... | $53,062 | ..... | $36.19 |

*Distribution of labor by operations.*— Plowing 1 time and harrowing 1.6 times required an average of 5.9 man hours and 12.3 horse hours per acre (table 41). Planting the crop required an average of 14.1 man hours and 8.6 horse hours per acre. This included: planting potatoes, 4.8 man hours and 7 horse hours per acre; cutting seed, 8.4 man hours per acre; hauling all the fertilizer, and drilling the fertilizer on 397 acres, 0.9 man hour and 1.6 horse hours per acre.

TABLE 41. Distribution of Labor by Operations, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Number of times over the ground | Total hours of labor | | Average hours of labor per acre | |
|---|---|---|---|---|---|
| | | Man | Horse | Man | Horse |
| Plowing | 1.0 | 6,416 | 13,669 | 4.4 | 9.3 |
| Fitting | 1.6 | 2,269 | 4,403 | 1.5 | 3.0 |
| Planting | ..... | 20,735 | 12,664 | 14.1 | 8.6 |
| Recovering | 0.3 | 847 | 1,489 | 0.6 | 1.0 |
| Weeding and harrowing | 3.7 | 4,983 | 5,687 | 3.4 | 3.9 |
| Cultivating | 3.5 | 9,927 | 17,486 | 6.8 | 11.9 |
| Hilling | 1.1 | 2,951 | 3,453 | 2.0 | 2.4 |
| Hoeing | 0.5 | 7,174 | ..... | 4.9 | ..... |
| Spraying | 1.7 | 1,736 | 1,851 | 1.2 | 1.3 |
| Harvesting | ..... | 58,961 | 26,941 | 40.2 | 18.4 |
| Marketing | ..... | 41,223 | 82,710 | 28.1 | 56.4 |
| Total hours | ..... | 157,222 | 170,353 | 107.2 | 116.2 |

The cultural operations consisted of recovering, weeding and harrowing, cultivating, hilling, and hoeing. The cultural practice differed from that in Steuben County by recovering and hilling less, and weeding and hoeing much more.

Spraying required an average of 1.2 man hours and 1.3 horse hours per acre.

Harvesting the potato crop required 40.2 man hours and 18.4 horse hours per acre. Marketing, including sorting and hauling by truck to New York or Brooklyn markets, required an average of 28.1 man hours and 56.4 horse hours per acre.

### *Use of equipment*

The use of equipment was estimated to be 5 cents per horse hour, the same rate that was used in the preceding counties. The total cost for use of equipment was $8518, or $5.81 per acre.

### *Miscellaneous items*

Miscellaneous items included: cash expenses of marketing, $8725, or $5.95 per acre; average annual expense for baskets, $1282, or 87 cents per acre; dust for cut seed, $112, or 8 cents per acre; formaldehyde for treating seed, $2. The total cost of miscellaneous items was $10,121, or an average of $6.90 per acre.

### *Returns from the potato crop*

A total of 274,364 bushels of potatoes was disposed of, worth $205,520 (table 42). Of these, 2122 bushels were used for seed, 2716 bushels were used in the house, and 436 bushels were fed to stock. The average value of the crop was 75 cents per bushel.

TABLE 42. YIELD AND VALUE OF POTATOES, 41 FARMS, 1466.3 ACRES, NASSAU COUNTY, 1912

| | Total | Average per acre |
|---|---|---|
| Bushels | 274,364 | 187 |
| Value | $205,520 | $140.16 |

*Summary of costs, returns, and profits*

The average farmer in Nassau County grew and marketed potatoes for 61 cents per bushel. The average cost of growing per bushel was 52 cents, the same as for Suffolk County. The summary of costs, returns, and profits is given in table 43:

TABLE 43. Summary of Costs, Returns, and Profits of Growing and Marketing Potatoes, 41 Farms, 1466.3 Acres, Nassau County, 1912

| | Total | Average per acre | Per cent of total cost |
|---|---|---|---|
| COSTS | | | |
| Seed | $22,398 | $15.28 | 13.5 |
| Manure | 2,461 | 1.68 | 1.5 |
| Fertilizer | 45,101 | 30.76 | 27.1 |
| Spray materials | 1,220 | 0.83 | 0.7 |
| Land rental | 23,140 | 15.78 | 13.9 |
| Use of buildings | 412 | 0.28 | 0.2 |
| Man labor | 27,510 | 18.76 | 16.5 |
| Horse labor | 25,552 | 17.43 | 15.4 |
| Use of equipment | 8,518 | 5.81 | 5.1 |
| Miscellaneous items | 10,121 | 6.90 | 6.1 |
| Cost of growing and marketing | $166,433 | $113.51 | 100.0 |
| Cost of growing without marketing | 142,677 | 97.30 | |
| Cost of marketing | 23,756 | 16.20 | |
| RETURNS | | | |
| Potatoes, 274,364 bushels | $205,520 | $140.16 | |
| PROFITS | $39,087 | $26.66 | |

*Probable error in total cost.*— The probable error in the cost per acre of growing and marketing potatoes in Nassau County is $\pm 0.257$, making this cost $\$113.51 \pm 0.257$.

SUMMARY OF COST OF PRODUCTION IN ALL AREAS

The three upstate areas compare very favorably with the other areas studied, in the cost per acre of production. The use of seed per acre varied from 10.2 bushels, in Steuben County, to 14.7 bushels, on the cost-account farms (table 44). The low amount of seed used in Steuben County is probably due to the high cost of seed and a consequent lower

rate of planting. The high cost of seed, as shown in table 45, probably affected the Suffolk County and the Nassau County data in the same way.

TABLE 44. AMOUNT OF SEED, MANURE, AND FERTILIZER USED PER ACRE, MAN AND HORSE LABOR REQUIRED PER ACRE, AND YIELD PER ACRE, IN ALL AREAS

| | Steuben County, 1912 | Clinton and Franklin Counties, 1913 | Cost-account farms, 1913, 1914, and 1915 | Suffolk County, 1912 | Nassau County, 1912 |
|---|---|---|---|---|---|
| Seed (bushels) | 10.2 | 12.0 | 14.7 | 11.9 | 12.4 |
| Manure (tons) | 2.3 | 4.3 | *..... | 0.4 | 0.6 |
| Fertilizer (pounds) | 124.0 | 407.0 | 458.0 | 1,840.0 | 1,868.0 |
| Man labor (hours) | 79.6 | 122.6 | †73.1 | 77.4 | 107.2 |
| Horse labor (hours) | 85.0 | 102.8 | †74.5 | 68.2 | 116.2 |
| Yield per acre (bushels) | 121.7 | 179.3 | 125.6 | 157.6 | 187.0 |

* The record of the number of tons of manure chargeable to potatoes was not available.
† Marketing labor not included.

TABLE 45. COST PER ACRE OF GROWING AND MARKETING POTATOES IN STEUBEN, CLINTON AND FRANKLIN, SUFFOLK, AND NASSAU COUNTIES, AND COST PER ACRE OF GROWING POTATOES ON COST-ACCOUNT FARMS

| | Steuben County, 1912 | Clinton and Franklin Counties, 1913 | Cost-account farms, 1913, 1914, and 1915 | Suffolk County, 1912 | Nassau County, 1912 |
|---|---|---|---|---|---|
| Seed | $ 9.48 | $ 6.79 | $ 6.91 | $14.70 | $15.28 |
| Manure | 4.80 | 7.21 | 5.78 | 0.88 | 1.68 |
| Fertilizer | 1.66 | 5.77 | 5.58 | 28.01 | 30.76 |
| Spray materials | 0.20 | 0.22 | 0.92 | 1.30 | 0.83 |
| Land rental | 3.00 | 3.00 | 4.47 | 12.81 | 15.78 |
| Use of buildings | 0.81 | 2.08 | 1.18 | 0.50 | 0.28 |
| Man labor | 13.93 | 21.45 | 13.58 | 13.54 | 18.76 |
| Horse labor | 12.75 | 15.43 | 11.06 | 10.23 | 17.43 |
| Use of equipment | 4.25 | 5.14 | 3.29 | 3.41 | 5.81 |
| Miscellaneous items | 0.25 | 0.34 | 0.01 | 0.14 | 6.90 |
| Total cost | $51.13 | $67.43 | $52.78 | $85.52 | $113.51 |

The upstate farms used more manure because more was produced on the farms and because the use of manure in Suffolk and Nassau Counties

tended to produce scab. Much more fertilizer, however, was used in Suffolk and Nassau Counties, and more insecticide and more bordeaux were used in these counties than in the upstate areas. Land rental also was much higher in Suffolk and Nassau Counties.

The labor cost in the cost-account farms does not include marketing, and in Nassau County it includes trucking to the New York City and Brooklyn markets. Hence these data should not be compared with the corresponding data for the other areas. The cost in Suffolk County was even lower than that in Steuben County, due probably to the level topography and a lighter soil. The high cost in Clinton and Franklin Counties is due to the small size and the irregularity of the fields and to the stony soil.

The principal difference in cost between the Long Island areas and the upstate areas is due to the use of better seed and more fertilizer, and to a higher land rental on the Long Island farms.

## RELATION OF VARIOUS FACTORS TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, STEUBEN COUNTY, 1912

Any change in farm practice that is designed to better agricultural conditions should have an economic value. A change in practice should bring the farmer a larger cash profit. An application of manure or fertilizer, deep plowing, thoro preparation of the ground, an extra cultivation, or spraying with bordeaux, should not increase the yield merely, but should increase it to a sufficient degree to leave a profit after all the added costs for materials, labor, use of equipment for the operation, and caring for the increase in the crop, are deducted.

### *Measures of success*

There is no simple criterion of success in potato production. Several factors should always be considered. Perhaps the most important factors are cost per bushel, profit per acre, cost per acre, and yield per acre.

*Cost per bushel.*— The cost per acre divided by the yield per acre gives the cost per bushel. The margin between the cost per bushel and the value per bushel, multiplied by the yield per acre, gives the profit. As the yield per acre increases, the cost per acre may increase, and the margin between cost per bushel and value per bushel may become narrower and

the profit per acre remain the same. When the margin between cost and value is wide, the importance of cost per bushel is lessened. However, the margin between cost and value is normally rather narrow, and cost per bushel is a good measure of success.

*Profit per acre.*— As has been shown, profit depends on the price per bushel. Thus, conclusions from studies such as this depend much on the market price. The ten-year average December 1 price from 1906 to 1915 for New York State was 63 cents per bushel. The December 1 price in New York for 1912 was 58 cents per bushel, or 8 per cent below the ten-year average. The average price received by the farmers in Steuben County in 1912 was 44 cents per bushel, or 24 per cent below the December 1, 1912, price.

*Cost per acre.*— Cost per acre should not be used alone except when the factor has no influence on the yield. The cost per acre is often increased by a practice that brings better yields and better profits, and in such cases this factor would be a poor measure of success in potato production. However, when the factor has no influence on the yield, the cost per acre is of importance. In such cases the returns per acre would remain the same and a reduction in cost would increase the profit.

*Yield per acre.*— Yield per acre is an important measure of success. However, an increase in yield that is brought about by any change in practice should leave a profit after all the increased costs are paid.

### *Acreage in potatoes*

The average acreage in potatoes per farm, in Steuben County, was 14.7 acres. Many farms had two or more fields in potatoes, and therefore the average size of fields was less than this. Thirty-two per cent of

TABLE 46. RELATION OF ACREAGE IN POTATOES TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| Acres in potatoes | Number of farms | Total acres in potatoes | Average acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|
| 0.1– 7.5..... | 21 | 135.5 | 6.4 | 127 | $56.80 | $0.45 | —$3.40 |
| 7.6–10..... | 92 | 856.0 | 9.3 | 109 | 52.92 | 0.48 | — 5.36 |
| 10.1–15..... | 119 | 1,540.8 | 12.9 | 122 | 50.58 | 0.41 | 2.67 |
| 15.1–20..... | 76 | 1,369.8 | 18.0 | 129 | 50.88 | 0.39 | 5.57 |
| Over 20..... | 47 | 1,325.0 | 28.2 | 121 | 50.26 | 0.42 | 4.68 |

the farms grew 10 acres or less of potatoes, and 7 per cent grew over 25 acres. The relation of the acreage in potatoes to cost of production and to profit is shown in table 46.

The table shows that the acreage in potatoes per farm had no effect on the yield. The cost per acre decreased from $56.80, in the 0.1–7.5-acre group, to $50.58 in the 10.1–15-acre group. The cost per acre was about the same on farms raising larger acreages of potatoes as on farms raising from 10.1 to 15 acres.

As shown in table 47, the least labor per acre was required on the largest acreages. The combined cost per acre of fertilizer, manure, and seed

TABLE 47. Relation of Acreage in Potatoes to Hours of Labor, Cost of Fertilizer and Manure, and Use of Seed, 355 Farms, Steuben County, 1912

| Acres in potatoes | Man hours per acre | Horse hours per acre | Cost of fertilizer per acre | Cost of manure per acre | Bushels of seed per acre | Cost of seed per acre |
|---|---|---|---|---|---|---|
| 0.1– 7.5 | 87.7 | 92.7 | $1.71 | $8.34 | 9.6 | $8.57 |
| 7.6–10 | 85.2 | 90.1 | 1.39 | 5.50 | 10.0 | 8.94 |
| 10.1–15 | 79.9 | 83.9 | 1.03 | 5.39 | 9.8 | 9.31 |
| 15.1–20 | 79.0 | 84.0 | 1.87 | 4.66 | 10.1 | 9.39 |
| Over 20 | 75.5 | 83.4 | 2.31 | 3.41 | 10.8 | 10.20 |

was almost the same for the farms of over 20 acres as for farms of from 7.6 to 10 acres. The 0.1–7.5-acre group used more stable manure on potatoes, and thus increased the cost per acre on those farms.

TABLE 48. Relation of Acreage in Potatoes to Tillage Practice, 355 Farms, Steuben County, 1912

| Acres in potatoes | Depth of plowing (inches) | Number of times harrowed | Number of times rolled | Number of times recovered | Number of times weeded or planked | Number of times cultivated | Number of times hilled |
|---|---|---|---|---|---|---|---|
| 0.1– 7.5 | 6.6 | 3.1 | 0.6 | 0.6 | 1.0 | 4.6 | 2.3 |
| 7.6–10 | 6.5 | 3.1 | 0.5 | 0.7 | 0.8 | 3.8 | 2.0 |
| 10.1–15 | 6.4 | 2.9 | 0.5 | 0.7 | 1.0 | 3.7 | 1.9 |
| 15.1–20 | 6.6 | 3.0 | 0.3 | 0.6 | 1.3 | 4.3 | 1.9 |
| Over 20 | 6.7 | 2.9 | 0.5 | 0.6 | 1.3 | 4.2 | 2.0 |

The tillage practices on the small acreages were similar to those on the larger acreages. The relation of the acreage in potatoes to the tillage practice is shown in table 48. The depth of plowing and the number of

Acres of potatoes per farm

| Cost per bushel (cents) | 0.1–5 | 5.1–10 | 10.1–15 | 15.1–20 | 20.1–25 | 25.1–30 | 30.1–35 | 35.1–40 | 40.1–45 | 45.1–50 | 50.1–55 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | | | 2 | | | | | | | | | 2 |
| 21– 25 | | 1 | 6 | 3 | | | | | | | | 10 |
| 26– 30 | | 3 | 9 | 7 | 5 | | | | 1 | | | 25 |
| 31– 35 | | 14 | 13 | 14 | 2 | 3 | | | | | | 46 |
| 36– 40 | 2 | 7 | 20 | 13 | 4 | 2 | 1 | 1 | 1 | | | 51 |
| 41– 45 | | 17 | 24 | 13 | 2 | 5 | 1 | | | | | 62 |
| 46– 50 | | 10 | 9 | 11 | 3 | 2 | | 1 | | 1 | | 37 |
| 51– 55 | | 14 | 9 | 7 | 2 | 2 | 1 | | | | 1 | 36 |
| 56– 60 | 1 | 15 | 8 | 2 | 1 | 1 | | | | | | 28 |
| 61– 65 | | 9 | 4 | 3 | | | 1 | | | | | 17 |
| 66– 70 | 1 | 3 | 5 | | 1 | | | | | | | 10 |
| 71– 75 | | 3 | 4 | 1 | 2 | | | | | | | 10 |
| 76– 80 | | 4 | 1 | | | | | | | | | 5 |
| 81– 85 | | 2 | 1 | 1 | | | | | | | | 4 |
| 86– 90 | | 2 | | | | | | | | | | 2 |
| 91– 95 | | 2 | 1 | | | | | | | | | 3 |
| 96–100 | | 1 | | | | | | | | | | 1 |
| 101–105 | | | 1 | | | | | | | | | 1 |
| 106–110 | | | | | | | | | | | | |
| 111–115 | | 1 | | | | | | | | | | 1 |
| 116–120 | | | | 1 | | | | | | | | 1 |
| 121–125 | | | | | | | | | | | | |
| 126–130 | | | | | | | | | | | | |
| 131–135 | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | |
| 141–145 | | | 1 | | | | | | | | | 1 |
| 146–150 | | | | | | | | | | | | |
| 151–155 | | 1 | | | | | | | | | | 1 |
| 156–160 | | | | | | | | | | | | |
| 161–165 | | | | | | | | | | | | |
| 166–170 | | | 1 | | | | | | | | | 1 |
| Totals | 4 | 109 | 119 | 76 | 22 | 15 | 4 | 2 | 2 | 1 | 1 | 355 |

$r = -0.164 \pm 0.035$

FIG. 88. CORRELATION BETWEEN ACRES OF POTATOES PER FARM AND COST PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

times harrowed were fairly uniform for all groups. The larger acreages were weeded or planked a little more than the smaller acreages, but were hilled less.

The chief reason for cheaper production of potatoes on the larger acreages is in the more efficient use of man and horse labor. There is less unproductive work in getting machinery ready for use or in changing from one kind of work to another. There is less time lost in turning around in larger fields. On larger acreages more of the special potato machinery can be used profitably.

*Correlation between acres of potatoes per farm and cost per bushel.*— The coefficient of correlation between acres in potatoes and cost per bushel in Steuben County was $-0.164 \pm 0.035$. This indicates that when all the farms were considered there was a correlation between an increase in acreage and a decrease in cost per bushel. It is probable that if the acre groups had been smaller, the correlation for the farms growing 15 acres or less of potatoes would have been much higher.

The correlation chart (fig. 88) shows the distribution of the farms producing potatoes at different costs in the different acreage groups.

### *Size of farm as affecting cost and profit*

The average size of the farms studied in Steuben County was 146 acres. The relation of the size of farm to production, cost of production, and profit, is shown in table 49:

TABLE 49. Relation of Size of Farm to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Farm area (acres) | Number of farms | Average farm area (acres) | Acres in potatoes | Per cent of area in potatoes | Man hours per acre | Horse hours per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| 50 or less | 7 | 45 | 10.9 | 24 | 93.9 | 87.6 | 127 | $48.97 | $0.39 | $8.25 |
| 51–100 | 81 | 86 | 11.0 | 13 | 80.2 | 84.8 | 119 | 49.89 | 0.42 | 0.90 |
| 101–150 | 147 | 125 | 13.6 | 11 | 81.0 | 84.6 | 123 | 51.97 | 0.42 | 2.96 |
| 151–200 | 77 | 174 | 17.5 | 10 | 80.6 | 86.4 | 124 | 52.42 | 0.42 | 2.54 |
| Over 200 | 43 | 295 | 21.4 | 7 | 73.4 | 84.0 | 117 | 48.75 | 0.42 | 2.33 |

The cost of potatoes was nearly the same on large farms as on small farms in Steuben County. The larger farms had larger acreages in potatoes per farm but a smaller proportion of their area in potatoes. Potatoes required less labor per acre on the larger farms. This decrease in labor per acre can be accounted for by the larger acreages in potatoes on the larger farms.

Cost accounts have shown that the cost per hour of labor and the cost for use of equipment are less on large farms than on small farms. If the cost per hour of labor and the cost for use of equipment had been determined for each individual farm, instead of the same rates being used on all farms, the effect of size of farm on labor and equipment costs would have been shown more clearly.

The advantages of larger farms in potato production are, cheaper labor and lower cost for use of equipment, and generally a larger acreage of potatoes per farm.

*Rotation of crops*

All the farmers in the Steuben County area followed some kind of rotation. Potatoes were seldom grown on the same ground two years in succession. The rotation consisted commonly of potatoes, grain, and hay from one to three years. The grain most commonly used was oats. A few farmers devoted two years of the rotation to grain crops, which were usually oats followed by wheat or rye. The land was left in hay for varying periods. Of the 355 farmers, 326 left their land in hay for periods varying between two and four years, 22 left their land in hay for one year or from one to two years, and 7 left their land in hay for a period of four years or more. Since the first two years of the rotation are so uniform, the difference between the rotations may be measured by the number of years the land is left in sod. The relation is shown in table 50:

TABLE 50. RELATION OF YEARS IN SOD TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| Years in sod | Number of farms | Acres in potatoes | Cost of fertilizer per acre | Cost of manure per acre | Bushels of seed per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 or 1–2... | 22 | 19.2 | $4.19 | $2.93 | 11.7 | $11.77 | 142 | $55.87 | $0.39 | $12.17 |
| 2 or 2–3... | 217 | 14.6 | 1.69 | 4.56 | 10.1 | 9.57 | 122 | 51.02 | 0.42 | 1.96 |
| 3 or more. | 116 | 14.0 | 0.95 | 5.74 | 9.8 | 8.71 | 116 | 50.09 | 0.43 | 0.94 |

The farms with the shorter rotations had a larger proportion of their crop area in potatoes and had a larger acreage of potatoes per farm, and apparently were more highly specialized potato farms. Less manure was used, but this was made up by the use of more fertilizer. More

and better seed was used. All these factors contributed to produce an increase in yield of 26 bushels per acre on the farms where the land was left in sod for the shortest time. It is probable, however, that the greatest part of the increased yield was due to a larger proportion of clover in the one-year-old sod.

*Elevation of land*

As the native habitat of the potato is in a cool climate at a high elevation in the torrid zone or the temperate zones, it has been assumed that elevation is an important factor influencing the yield of potatoes. In general, each 300 feet increase in elevation decreases the mean yearly temperature 1 degree. The effect of the mean yearly temperature on potatoes is shown in table 51. In years when the temperature was below

TABLE 51. Relation of Temperature to Potato Yield, New York State, 1890–1915

| Number of years | Average departure from average annual mean (degrees) | Average yield of potatoes per acre (bushels) |
|---|---|---|
| 13 | —0.94 | 94.0 |
| 13 | +0.92 | 78.2 |
| Difference | 1.86 | 15.8 |

normal, averaging 0.94 degree below, the average yield in New York State was 94 bushels per acre; and when the temperature was above normal, averaging 0.92 degree above, the average yield was 78.2 bushels per acre. One degree decrease in mean yearly temperature increased the yield in New York State 8.5 bushels per acre, on the average. The difference in the yield between the less-than-1400-feet group and the 2000-feet-or-more group, shown in table 52, should be about 20 bushels if all other factors were eliminated. In Steuben County, however, the poorer soils were found at the higher elevations. The Lordstown silt loam and some Volusia silt loam were found above 1800 feet. The Lordstown loam was found from 1400 feet to 1800 feet. A better phase of the Lordstown loam and some Chenango loam were found below 1400 feet.

TABLE 52. RELATION OF ELEVATION TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| Elevation (feet) | Number of farms | Average elevation (feet) | Value of land per acre | Miles to market | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| Less than 1,400 | 46 | 1,321 | $63 | 1.7 | 12.5 | 152 | $54.93 | $0.36 | $9.72 |
| 1,400–1,599 | 85 | 1,483 | 65 | 2.7 | 14.7 | 122 | 49.97 | 0.41 | 2.98 |
| 1,600–1,799 | 108 | 1,689 | 50 | 3.6 | 14.1 | 117 | 49.89 | 0.43 | 1.65 |
| 1,800–1,999 | 95 | 1,862 | 45 | 3.9 | 16.4 | 116 | 51.72 | 0.45 | 0.40 |
| 2,000 or more | 21 | 2,033 | 44 | 5.1 | 14.9 | 115 | 51.77 | 0.45 | 1.37 |

In spite of the general effect of elevation on temperature and of temperature on potato yields, the better yields were obtained at the lower elevations in Steuben County. At the higher elevations less cultivating was done and the total time per acre spent on potatoes was less, as is shown in table 53. Aside from these differences the farm practice was about the same. The larger yields obtained at the lower elevations lowered the cost per bushel and gave a good profit.

TABLE 53. RELATION OF ELEVATION TO FARM PRACTICE, 355 FARMS, STEUBEN COUNTY, 1912

| Elevation (feet) | Man hours per acre | Horse hours per acre | Number of hills per acre | Depth of plowing (inches) | Bushels of seed per acre | Cost of seed per acre | Cost of fertilizer per acre | Cost of manure per acre |
|---|---|---|---|---|---|---|---|---|
| Less than 1,400 | 86.1 | 92.0 | 6,991 | 7.1 | 10.8 | $10.05 | $1.98 | $4.97 |
| 1,400–1,599 | 80.1 | 82.4 | 6,108 | 6.5 | 9.8 | 9.49 | 0.92 | 4.99 |
| 1,600–1,799 | 78.9 | 83.5 | 5,998 | 6.4 | 10.0 | 8.78 | 1.70 | 4.81 |
| 1,800–1,999 | 78.2 | 86.5 | 6,858 | 6.5 | 10.4 | 9.67 | 2.09 | 4.53 |
| 2,000 or more | 76.6 | 83.1 | 7,098 | 6.6 | 10.3 | 10.84 | 1.68 | 4.92 |

*Correlation between elevation of land and cost of potatoes per bushel.*— The coefficient of correlation between elevation and cost per bushel was $0.130 \pm 0.035$. The correlation chart (fig. 89) shows the distribution of the farms in this regard.

### *Value of farm*

The value of the farm per acre was governed mainly by fertility and by distance to market, and to a smaller extent by topography. The cheapest land was found on the tops of the hills. The soil was Lordstown or Volusia silt loam. It was usually located three miles or more from market. The highest-priced land was usually in the valleys near

market. As shown in table 54, the best potato yields were obtained on the highest-priced land. On land worth less than $40 per acre, potatoes were raised at a loss of $7.55 per acre.

| Cost per bushel (cents) | Elevation of land (feet) 1201–1300 | 1301–1400 | 1401–1500 | 1501–1600 | 1601–1700 | 1701–1800 | 1801–1900 | 1901–2000 | 2001–2100 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | | 1 | | | | | 1 | | | 2 |
| 21– 25 | | 3 | 2 | 2 | 2 | 1 | | | | 10 |
| 26– 30 | 1 | 2 | 4 | 3 | 5 | 5 | 2 | 3 | | 25 |
| 31– 35 | 2 | 12 | 4 | 5 | 6 | 9 | 4 | 2 | 2 | 46 |
| 36– 40 | 2 | 5 | 5 | 9 | 6 | 6 | 10 | 5 | 3 | 51 |
| 41– 45 | 5 | 10 | 6 | 12 | 10 | 7 | 6 | 4 | 2 | 62 |
| 46– 50 | 2 | 6 | 3 | 5 | 4 | 7 | 7 | 3 | | 37 |
| 51– 55 | 1 | 3 | 8 | 2 | 5 | 8 | 6 | 1 | 2 | 36 |
| 56– 60 | | 1 | 2 | 3 | 5 | 7 | 9 | | 1 | 28 |
| 61– 65 | | 3 | 2 | | 2 | 7 | | 2 | 1 | 17 |
| 66– 70 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | | 1 | 10 |
| 71– 75 | 1 | | 1 | | 2 | 2 | 2 | 1 | 1 | 10 |
| 76– 80 | | | | 2 | | 1 | | 1 | 1 | 5 |
| 81– 85 | | | | 1 | 1 | | 1 | 1 | | 4 |
| 86– 90 | | | | | 2 | | | | | 2 |
| 91– 95 | | 1 | | 1 | | 1 | | | | 3 |
| 96–100 | | | | | | | 1 | | | 1 |
| 101–105 | | | | | | 1 | | | | 1 |
| 106–110 | | | | | | | | | | |
| 111–115 | | | | | | | | 1 | | 1 |
| 116–120 | | | | 1 | | | | | | 1 |
| 121–125 | | | | | | | | | | |
| 126–130 | | | | | | | | | | |
| 131–135 | | | | | | | | | | |
| 136–140 | | | | | | | | | | |
| 141–145 | | 1 | | | | | | | | 1 |
| 146–150 | | | | | | | | | | |
| 151–155 | | | | | | | 1 | | | 1 |
| 156–160 | | | | | | | | | | |
| 161–165 | | | | | | | | | | |
| 166–170 | | | | | | 1 | | | | 1 |
| Totals | 15 | 49 | 38 | 47 | 52 | 64 | 52 | 24 | 14 | 355 |

$r = 0.130 \pm 0.035$

FIG. 89. CORRELATION BETWEEN ELEVATION OF LAND AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

Farms valued at from $60 to $99 per acre gave the highest profit per acre, $6.52. On higher-priced farms the profit per acre was $6.34.

TABLE 54. RELATION OF VALUE OF FARM PER ACRE TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| Value of farm per acre | Number of farms | Average value of farm per acre | Elevation (feet) | Miles to market | Number of hills per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|---|
| Less than $40.... | 46 | $ 32 | 1,711 | 4.2 | 5,951 | 92 | $48.84 | $0.53 | —$7.55 |
| $40–$59..... | 185 | 45 | 1,719 | 3.6 | 6,443 | 120 | 51.08 | 0.43 | 2.20 |
| $60–$99..... | 102 | 71 | 1,572 | 2.8 | 6,846 | 135 | 52.48 | 0.39 | 6.52 |
| $100 or more..... | 22 | 102 | 1,440 | 1.7 | 5,689 | 139 | 49.86 | 0.36 | 6.34 |

The differences between profits were somewhat exaggerated by the use of a uniform rental charge for all farms. If rental had been based on actual value, the profit on the low-priced farms would have been somewhat higher and on the high-priced farms somewhat lower. Farm practice did not differ greatly on the high- and the low-priced farms, but the farmers operating the high-priced farms used better seed and plowed about half an inch deeper. The amount of labor required on the different grades of farms was very similar.

*Correlation between value of farm and cost of potatoes per bushel.*— The coefficient of correlation between value of farm per acre and cost of potatoes per bushel was $-0.296 \pm 0.033$. This indicates that as the value of the farm per acre increased, the cost of potatoes per bushel tended to decrease. The distribution of the farms in this respect is shown by the correlation chart (fig. 90).

### *Miles to market*

Potatoes are a bulky crop. Distance to market may be a limiting factor in their production. This disadvantage was lessened in Steuben County by marketing the potatoes in the winter, when labor was not otherwise employed. By thus avoiding the conflict between harvesting and marketing labor, the farmers at a distance from market were able to grow nearly as large acreages of potatoes as those near market. Of the total crop sold on 355 farms, 62 per cent was marketed from storage. A part of the potatoes sold from storage were not sold until the following April and May, when the roads were heavy and when the farmers' labor could have been more profitably employed.

The cost of hauling per bushel, for farms located two miles or less from the railway station, was $3\frac{1}{2}$ cents, and for farms located over six miles

Value of farm per acre

| Cost per bushel (cents) | $21– $30 | $31– $40 | $41– $50 | $51– $60 | $61– $70 | $71– $80 | $81– $90 | $91–$100 | $101–$110 | $111–$120 | $121–$130 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | | 1 | | | | 1 | | | | | | 2 |
| 21– 25 | | 1 | 1 | 2 | 1 | 1 | 1 | 3 | | | | 10 |
| 26– 30 | 1 | 7 | 7 | 3 | 2 | 1 | | 3 | | | 1 | 25 |
| 31– 35 | 1 | 10 | 10 | 7 | 4 | 9 | 3 | 2 | | | | 46 |
| 36– 40 | | 12 | 14 | 8 | 4 | 9 | | 4 | | | | 51 |
| 41– 45 | 4 | 19 | 14 | 5 | 4 | 11 | | 5 | | | | 62 |
| 46– 50 | 3 | 11 | 9 | 6 | 4 | 2 | 1 | 1 | | | | 37 |
| 51– 55 | 3 | 16 | 8 | 4 | | 3 | | 2 | | | | 36 |
| 56– 60 | 3 | 12 | 6 | 4 | | 2 | | | | | 1 | 28 |
| 61– 65 | 3 | 8 | 3 | 2 | 1 | | | | | | | 17 |
| 66– 70 | 1 | 5 | 2 | | | 1 | | 1 | | | | 10 |
| 71– 75 | | 4 | 3 | 2 | | 1 | | | | | | 10 |
| 76– 80 | 2 | 1 | 2 | | | | | | | | | 5 |
| 81– 85 | 1 | 2 | | 1 | | | | | | | | 4 |
| 86– 90 | | 1 | 1 | | | | | | | | | 2 |
| 91– 95 | 1 | 1 | | 1 | | | | | | | | 3 |
| 96–100 | | | | 1 | | | | | | | | 1 |
| 101–105 | | 1 | | | | | | | | | | 1 |
| 106–110 | | | | | | | | | | | | |
| 111–115 | 1 | | | | | | | | | | | 1 |
| 116–120 | | 1 | | | | | | | | | | 1 |
| 121–125 | | | | | | | | | | | | |
| 126–130 | | | | | | | | | | | | |
| 131–135 | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | |
| 141–145 | 1 | | | | | | | | | | | 1 |
| 146–150 | | | | | | | | | | | | |
| 151–155 | 1 | | | | | | | | | | | 1 |
| 156–160 | | | | | | | | | | | | |
| 161–165 | | | | | | | | | | | | |
| 166–170 | | 1 | | | | | | | | | | 1 |
| Totals | 26 | 114 | 80 | 46 | 20 | 41 | 5 | 21 | | | 2 | 355 |

$r = -0.296 \pm 0.033$

FIG. 90. CORRELATION BETWEEN VALUE OF FARM PER ACRE AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

from the station it was 6.7 cents (table 55). The greatest profit per acre was made by the farmers who were located two miles or less from market. Such farms, however, were situated at a lower elevation and had a better soil.

TABLE 55. RELATION OF MILES TO MARKET TO COST OF HAULING TO MARKET, COST OF GROWING AND MARKETING, AND PROFIT, 289 FARMS, STEUBEN COUNTY, 1912*

| Miles to market | Number of farms | Acres in potatoes | Average miles to market† | Value of land per acre | Man hours hauling per 100 bushels | Horse hours hauling per 100 bushels | Cost of labor and equipment for hauling per bushel | Cost of growing and marketing per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|---|
| 2 or less | 86 | 14.8 | 1.5 | $57 | 6.2 | 12.3 | $0.035 | $0.38 | $7.04 |
| 2.1–4 | 118 | 15.9 | 3.2 | 54 | 8.6 | 18.0 | 0.051 | 0.43 | 1.67 |
| 4.1–6 | 69 | 15.0 | 5.0 | 44 | 10.4 | 21.1 | 0.060 | 0.47 | — 2.50 |
| Over 6 | 16 | 12.1 | 7.3 | 38 | 11.6 | 23.2 | 0.067 | 0.47 | 0.27 |

* In some of the records of the 355 farms studied in Steuben County, the marketing labor was included with the digging labor. This table includes only the farms where the labor was separated on the original blank. The accompanying chart (fig. 91) includes all the 355 farms.
† Weighted according to bushels marketed.

*Correlation between miles to market and cost of potatoes per bushel.*— The coefficient of correlation between miles to market and cost of potatoes per bushel was $0.244 \pm 0.034$. This indicates that an increase in distance was accompanied by an increase in the cost per bushel. The distribution is shown by the correlation chart (fig. 91).

### *Manure*

Potato yields in Steuben County in 1912 were increased by the use of manure. However, as shown in table 56, when more than $8 worth of manure per acre was used, the increase in yield was not enough to pay for the increase in cost. On farms using more than $8 worth of manure per acre, the average cost per bushel was higher and the profit was lower

TABLE 56. RELATION OF THE USE OF MANURE TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 108 FARMS, STEUBEN COUNTY, 1912

(The first group received no manure. The second and third groups received manure on 75 per cent or more of the area in potatoes)

| Cost of application per acre | Number of farms | Acres in potatoes | Cost of manure per acre | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|
| 0 (No manure applied) | 23 | 11.5 | $ 0.09 | $1.02 | 91 | $44.14 | $0.47 | —$4.07 |
| $0.01–$8 | 46 | 12.7 | 5.78 | 0.89 | 131 | 51.13 | 0.39 | 6.63 |
| Over $8 | 39 | 10.9 | 11.02 | 0.66 | 146 | 58.03 | 0.40 | 2.80 |

than on farms using less manure. The application of manure up to $8 worth per acre increased the profit by $1.85, on the average, for each

| Cost per bushel (cents) | Miles to market 0.1–1 | 1.1–2 | 2.1–3 | 3.1–4 | 4.1–5 | 5.1–6 | 6.1–7 | 7.1–8 | 8.1–9 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | | 1 | 1 | | | | | | | 2 |
| 21– 25 | 2 | 4 | 3 | 1 | | | | | | 10 |
| 26– 30 | 3 | 12 | 3 | 3 | 1 | 2 | | 1 | | 25 |
| 31– 35 | 3 | 15 | 10 | 10 | 3 | 2 | 3 | | | 46 |
| 36– 40 | 5 | 7 | 15 | 8 | 12 | 2 | | 2 | | 51 |
| 41– 45 | 7 | 13 | 19 | 10 | 9 | 2 | 2 | | | 62 |
| 46– 50 | 3 | 8 | 10 | 6 | 8 | | 1 | 1 | | 37 |
| 51– 55 | | 9 | 7 | 6 | 8 | 3 | 2 | 1 | | 36 |
| 56– 60 | 1 | 8 | 7 | 5 | 5 | | 2 | | | 28 |
| 61– 65 | 2 | 3 | | 6 | 4 | 1 | 1 | | | 17 |
| 66– 70 | 1 | 2 | 2 | | 4 | | 1 | | | 10 |
| 71– 75 | | 1 | 3 | 1 | 3 | 1 | | 1 | | 10 |
| 76– 80 | | 1 | 1 | 1 | | 1 | | 1 | | 5 |
| 81– 85 | | 1 | 1 | 1 | 1 | | | | | 4 |
| 86– 90 | | | | | 2 | | | | | 2 |
| 91– 95 | | | 2 | 1 | | | | | | 3 |
| 96–100 | | | | 1 | | | | | | 1 |
| 101–105 | | | | | | 1 | | | | 1 |
| 106–110 | | | | | | | | | | |
| 111–115 | | | | | | | | | 1 | 1 |
| 116–120 | | | | 1 | | | | | | 1 |
| 121–125 | | | | | | | | | | |
| 126–130 | | | | | | | | | | |
| 131–135 | | | | | | | | | | |
| 136–140 | | | | | | | | | | |
| 141–145 | | 1 | | | | | | | | 1 |
| 146–150 | | | | | | | | | | |
| 151–155 | | | | | | | | 1 | | 1 |
| 156–160 | | | | | | | | | | |
| 161–165 | | | | | | | | | | |
| 166–170 | | | | | | 1 | | | | 1 |
| Totals | 27 | 86 | 84 | 61 | 60 | 16 | 12 | 8 | 1 | 355 |

$r = 0.244 \pm 0.034$

FIG. 91. CORRELATION BETWEEN MILES TO MARKET AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

dollar spent for manure (table 57). The application of manure beyond $8 worth per acre decreased the profit by 73 cents for each dollar of increase in value of manure applied. Apparently, therefore, the farmer who

applied more than $8 worth of manure per acre would have made more if the manure had been applied to twice the area.

TABLE 57. RELATION OF INCREASE IN APPLICATION OF MANURE TO INCREASE IN YIELD AND INCREASE IN PROFIT, 108 FARMS, STEUBEN COUNTY, 1912

| Cost of application per acre | Average cost of application per acre | Increase in cost per acre over preceding group | Increase in yield per dollar increase in cost of manure (bushels) | Increase or decrease in profit per dollar increase in cost of manure |
|---|---|---|---|---|
| 0 | $ 0.00 | ..... | ..... | ..... |
| $0.01–$8 | 5.78 | $5.78 | 6.4 | $1.85 |
| Over $8 | 11.02 | 5.24 | 2.9 | — 0.73 |

*Fertilizer*

Fertilizer was largely used to supplement farm manure in Steuben County. Where farm manure was applied to 75 per cent or more of the potato land, the fertilizer cost per acre was only 79 cents; where farm manure was applied to less than 75 per cent of the potato land, the average cost of fertilizer per acre was $1.87. The farmers who used fertilizer received the best yields, as is shown in table 58. Where no fertilizer was

TABLE 58. RELATION OF THE USE OF FERTILIZER TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| Cost of application per acre | Number farms | Acres in potatoes | Per cent of area fertilized | Cost of fertilizer per acre | Cost of manure per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 0 (No fertilizer applied) | 208 | 13.5 | 0 | $ 0.00 | $5.17 | 114 | $48.48 | $0.43 | $0.58 |
| $0.01–$4 | 92 | 16.2 | 50 | 2.08 | 4.49 | 121 | 50.67 | 0.42 | 3.23 |
| $4.01–$8 | 47 | 17.1 | 86 | 5.30 | 4.10 | 145 | 59.05 | 0.41 | 6.92 |
| Over $8 | 8 | 15.8 | 93 | 10.41 | 4.53 | 158 | 64.70 | 0.41 | 6.95 |

used the yield per acre was 114 bushels; where up to $4 worth of fertilizer was used the yield per acre was 121 bushels; where from $4.01 to $8 worth was applied the yield per acre was 145 bushels; and where over $8 worth was applied the yield per acre was 158 bushels. Where more than $8 worth of fertilizer was applied per acre the increase in the yield was only

enough to pay for the increased cost of production. The increase in yield for each dollar of increase in the cost of fertilizer application was greatest when from $4.01 to $8 worth of fertilizer was applied per acre (table 59). The increase in profit for each dollar of increase in the cost

TABLE 59. Relation of Increase in Application of Fertilizer to Increase in Yield and Increase in Profit, 355 Farms, Steuben County, 1912

| Cost of application per acre | Average cost of application per acre | Increase in cost per acre over preceding group | Increase in yield per dollar increase in cost of fertilizer (bushels) | Increase in profit per dollar increase in cost of fertilizer |
|---|---|---|---|---|
| 0 | $ 0.00 | ..... | ..... | ..... |
| $0.01–$4 | 2.08 | $2.08 | 3.4 | $1.27 |
| $4.01–$8 | 5.30 | 3.22 | 7.5 | 1.15 |
| Over $8 | 10.41 | 5.11 | 2.5 | 0.01 |

of fertilizer application was greatest where up to $4 worth of fertilizer was applied per acre, and this increase was nearly as great when from $4.01 to $8 worth of fertilizer was applied. Evidently the most profitable rate of fertilizer application in Steuben County was from $2 to $5 worth per acre.

*Depth of plowing*

The usual recommendation is to plow deeply, thus increasing the depth of the topsoil and furnishing a loose soil for the development of the potato roots. The depth of plowing in Steuben County varied from 4 to 9 inches. Fifty-one farms plowed less than 6 inches deep, and 49 plowed 8 inches deep or more (table 60). The average depth of plowing was 6.6 inches.

TABLE 60. Relation of Depth of Plowing to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Depth of plowing (inches) | Number of farms | Average depth of plowing (inches) | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|
| Less than 6 | 51 | 5.0 | 14.8 | 107 | $48.95 | $0.46 | —$2.52 |
| 6–6.9 | 130 | 6.1 | 14.2 | 113 | 49.52 | 0.44 | — 0.30 |
| 7–7.9 | 125 | 7.1 | 15.3 | 131 | 52.37 | 0.40 | 6.19 |
| 8 or more | 49 | 8.1 | 14.4 | 135 | 54.26 | 0.40 | 4.92 |

FIG. 92. PLOWING FOR POTATOES IN STEUBEN COUNTY

The two-way sulky plow is to the hills of New York what the gang plow is to the prairies of the West. It is usually drawn by three horses. The growth of weeds and hay that is being turned under should be noted.

The farms that plowed deeper than the average were on a little better land and used a little more fertilizer, manure, and seed, as is shown in table 61. All these conditions contributed to the increase in yield.

TABLE 61. RELATION OF DEPTH OF PLOWING TO VALUE OF LAND, ELEVATION, AND USE OF FERTILIZER, MANURE, AND SEED, 355 FARMS, STEUBEN COUNTY, 1912

| Depth of plowing (inches) | Value of land per acre | Elevation (feet) | Cost of fertilizer per acre | Cost of manure per acre | Bushels of seed per acre | Cost of seed per acre |
|---|---|---|---|---|---|---|
| Less than 6 | $51 | 1,670 | $1.10 | $4.53 | 10.1 | $ 8.97 |
| 6–6.9 | 50 | 1,673 | 1.52 | 4.63 | 9.9 | 8.97 |
| 7–7.9 | 54 | 1,669 | 1.89 | 4.87 | 10.4 | 10.00 |
| 8 or more | 61 | 1,583 | 1.98 | 5.30 | 10.4 | 9.94 |

The increase in cost of production due to deeper plowing was very small, as is shown in table 62. The increase from 5 inches to 8.1 inches in depth of plowing, an increase of 3.1 inches, added 36 cents per acre to the cost for man and horse labor and for use of equipment.

TABLE 62. Relation of Depth of Plowing to Hours of Labor and Cost of Plowing, 355 Farms, Steuben County, 1912

| Depth of plowing (inches) | Average depth of plowing (inches) | Total man hours per acre | Total horse hours per acre | Man hours plowing per acre | Horse hours plowing per acre | Cost of plowing per acre |
|---|---|---|---|---|---|---|
| Less than 6 | 5.0 | 80.0 | 81.1 | 5.8 | 12.8 | $3.58 |
| 6–6.9 | 6.1 | 78.4 | 82.3 | 5.8 | 13.5 | 3.72 |
| 7–7.9 | 7.1 | 79.9 | 86.8 | 5.8 | 13.6 | 3.74 |
| 8 or more | 8.1 | 81.5 | 91.5 | 5.6 | 14.8 | 3.94 |

*Correlation between depth of plowing and cost of potatoes per bushel.*— The coefficient of correlation between depth of plowing and cost of potatoes per bushel was $-0.218 \pm 0.034$. This indicates a tendency for the cost per bushel to decrease as the depth of plowing increased. The distribution of the farms in this respect is shown by the correlation chart (fig. 93).

*Fitting*

After plowing, part of the land was rolled. Most of the ground was pulverized with spring-tooth harrows. A few farmers used disk harrows. Only one farmer harrowed less than 2 times and eleven harrowed 5 or more times. The largest number of the farmers harrowed 3 times (table 63).

TABLE 63. Relation of Number of Times Harrowed to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Number of times harrowed | Number of farms | Average number of times harrowed | Depth of plowing (inches) | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|
| Less than 3 | 85 | 2.1 | 6.3 | 14.5 | 118 | $47.28 | $0.40 | $3.53 |
| 3–3.9 | 217 | 3.0 | 6.6 | 15.2 | 121 | 51.42 | 0.42 | 2.47 |
| 4–4.9 | 42 | 4.0 | 6.9 | 13.9 | 133 | 55.48 | 0.42 | 2.40 |
| 5 or more | 11 | 6.1 | 6.6 | 10.8 | 123 | 61.37 | 0.50 | — 8.43 |

The eleven farmers who harrowed 5 times or more had quack grass or other unusual conditions to contend with, and perhaps should not be considered here except as the increased harrowings have limited the profit. An increase in the number of harrowings from less than 3 up to 5 resulted

in increased yields. The depth of plowing also was increased, and there was a tendency to use more fertilizer and more and better seed. The

| Cost per bushel (cents) | Depth plowed (inches) 3.1–4 | 4.1–5 | 5.1–6 | 6.1–7 | 7.1–8 | 8.1–9 | Totals |
|---|---|---|---|---|---|---|---|
| 16– 20 | | | 1 | | 1 | | 2 |
| 21– 25 | | 1 | 2 | 3 | 3 | 1 | 10 |
| 26– 30 | | 4 | 2 | 16 | 3 | | 25 |
| 31– 35 | | 2 | 16 | 18 | 10 | | 46 |
| 36– 40 | 1 | 6 | 15 | 20 | 9 | | 51 |
| 41– 45 | 1 | 3 | 24 | 24 | 9 | 1 | 62 |
| 46– 50 | 1 | 7 | 14 | 10 | 3 | 2 | 37 |
| 51– 55 | 1 | 3 | 9 | 16 | 6 | 1 | 36 |
| 56– 60 | | 3 | 12 | 7 | 6 | | 28 |
| 61– 65 | 1 | | 7 | 8 | 1 | | 17 |
| 66– 70 | | 1 | 3 | 4 | 2 | | 10 |
| 71– 75 | | 1 | 3 | 4 | 2 | | 10 |
| 76– 80 | | 1 | 1 | 3 | | | 5 |
| 81– 85 | | | 2 | 1 | 1 | | 4 |
| 86– 90 | | | 1 | | 1 | | 2 |
| 91– 95 | | | 1 | | 2 | | 3 |
| 96–100 | | | | 1 | | | 1 |
| 101–105 | | | | 1 | | | 1 |
| 106–110 | | | | | | | |
| 111–115 | | | 1 | | | | 1 |
| 116–120 | | 1 | | | | | 1 |
| 121–125 | | | | | | | |
| 126–130 | | | | | | | |
| 131–135 | | | | | | | |
| 136–140 | | | | | | | |
| 141–145 | | | | 1 | | | 1 |
| 146–150 | | | | | | | |
| 151–155 | | | 1 | | | | 1 |
| 156–160 | | | | | | | |
| 161–165 | | | | | | | |
| 166–170 | | 1 | | | | | 1 |
| Totals | 5 | 34 | 115 | 137 | 59 | 5 | 355 |

$r = -0.218 \pm 0.034$

FIG. 93. CORRELATION BETWEEN DEPTH OF PLOWING AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

increase in yield, however, was not enough to pay the increased costs. The farmers who harrowed less than 3 times had the highest average profit per acre in spite of a low average yield.

The cost of harrowing per acre was about 80 cents for each time over. The farmers who harrowed their ground the most also spent more time on other operations, as is shown in table 64:

TABLE 64. Relation of Number of Times Harrowed to Total Hours of Labor and Cost of Harrowing, 355 Farms, Steuben County, 1912

| Number of times harrowed | Total man hours per acre | Total horse hours per acre | Man hours harrowing per acre | Horse hours harrowing per acre | Cost of harrowing per acre |
|---|---|---|---|---|---|
| Less than 3 | 75.5 | 79.0 | 2.2 | 5.6 | $1.50 |
| 3–3.9 | 79.7 | 85.3 | 3.3 | 8.6 | 2.30 |
| 4–4.9 | 84.8 | 92.3 | 4.4 | 11.8 | 3.13 |
| 5 or more | 94.0 | 104.4 | 7.6 | 19.0 | 5.13 |

*Correlation between number of times harrowed and cost of potatoes per bushel.*—The coefficient of correlation between the number of times harrowed and the cost of potatoes per bushel was $0.114 \pm 0.035$. This indicates a tendency for the cost per bushel to increase as the number of harrowings increased. The correlation chart (fig. 94) shows the distribution of the farms in this regard.

### *Date of planting*

The potatoes that were planted earliest in 1912 in Steuben County rotted the least, evidently maturing before being severely attacked by late blight. This is shown in table 65. If there had been no losses thru

TABLE 65. Relation of Date of Planting to Production, Cost of Production, and Profit, 210 Farms, Steuben County, 1912

| Date of planting | Number of farms | Acres in potatoes | Estimated field rot (not harvested) per acre (bushels) | Average total yield harvested per acre (bushels) | Average yield per acre allowing for all losses (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|
| Before May 15 | 10 | 11.7 | 10 | 144 | 132 | $53.81 | $0.41 | $6.34 |
| May 15–31 | 150 | 13.2 | 23 | 139 | 126 | 51.43 | 0.41 | 3.48 |
| June 1 or after | 50 | 12.1 | 36 | 116 | 94 | 50.02 | 0.53 | — 8.15 |

late blight the highest yields would have been obtained by the farmers who planted their potatoes between May 15 and May 31.

| Cost per bushel (cents) | Number of times harrowed | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1–1.9 | 2–2.9 | 3–3.9 | 4–4.9 | 5–5.9 | 6–6.9 | 7–7.9 | 8–8.9 | 9–9.9 | |
| 16– 20 | | 1 | | 1 | | | | | | 2 |
| 21– 25 | 1 | 5 | 3 | 1 | | | | | | 10 |
| 26– 30 | | 6 | 16 | 2 | 1 | | | | | 25 |
| 31– 35 | | 14 | 27 | 4 | | | | 1 | | 46 |
| 36– 40 | | 14 | 35 | 2 | | | | | | 51 |
| 41– 45 | | 9 | 38 | 12 | 2 | 1 | | | | 62 |
| 46– 50 | | 9 | 24 | 4 | | | | | | 37 |
| 51– 55 | | 6 | 26 | 3 | | 1 | | | | 36 |
| 56– 60 | | 8 | 13 | 6 | | | | | 1 | 28 |
| 61– 65 | | 3 | 13 | | 1 | | | | | 17 |
| 66– 70 | | 3 | 4 | 3 | | | | | | 10 |
| 71– 75 | | 1 | 5 | 3 | | | | 1 | | 10 |
| 76– 80 | | | 4 | 1 | | | | | | 5 |
| 81– 85 | | | 4 | | | | | | | 4 |
| 86– 90 | | 1 | | | | | 1 | | | 2 |
| 91– 95 | | 1 | 2 | | | | | | | 3 |
| 96–100 | | | 1 | | | | | | | 1 |
| 101–105 | | 1 | | | | | | | | 1 |
| 106–110 | | | | | | | | | | |
| 111–115 | | | 1 | | | | | | | 1 |
| 116–120 | | 1 | | | | | | | | 1 |
| 121–125 | | | | | | | | | | |
| 126–130 | | | | | | | | | | |
| 131–135 | | | | | | | | | | |
| 136–140 | | | | | | | | | | |
| 141–145 | | | 1 | | | | | | | 1 |
| 146–150 | | | | | | | | | | |
| 151–155 | | 1 | | | | | | | | 1 |
| 156–160 | | | | | | | | | | |
| 161–165 | | | | | | | | | | |
| 166–170 | | | | | 1 | | | | | 1 |
| Totals | 1 | 84 | 217 | 42 | 5 | 2 | 1 | 2 | 1 | 355 |

$r = 0.114 \pm 0.035$

FIG. 94. CORRELATION BETWEEN NUMBER OF TIMES HARROWED AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

*Depth of planting*

The depth at which potatoes are planted has little effect on the yield. If potatoes are planted too deep or too shallow, the plants tend to root

at a proper level. Too shallow planting tends to expose some of the tubers, resulting in green potatoes which are not marketable. On the other hand, planting too deep increases the time between the planting and the coming up, and also increases the amount of labor required to harvest the crop. Little difference in cost is shown within the limits of the three groups given in table 66. More than half of the farmers

TABLE 66. Relation of Depth of Planting to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Depth of planting (inches) | Number of farms | Average depth of planting (inches) | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| 2 or less | 59 | 1.9 | 15.2 | 120 | $51.45 | $0.43 | $0.17 |
| 2.1–3 | 180 | 2.9 | 14.8 | 125 | 51.63 | 0.41 | 3.60 |
| Over 3 | 116 | 4.0 | 14.4 | 118 | 50.15 | 0.43 | 1.90 |

planted their potatoes between 2.1 and 3 inches deep. These farmers obtained the best yields and made the highest profits.

*Correlation between depth of planting and cost of potatoes per bushel.*— The coefficient of correlation between depth of planting and cost of potatoes per bushel was $0.001 \pm 0.036$, which indicates no correlation. The distribution of farms is shown in the correlation chart (fig. 95).

### *Number of hills per acre*

The farms that had over 9000 hills per acre, which is equivalent to planting 20 inches apart in rows 34 inches apart, received the largest yields and the best profits, as is shown in table 67. On most of the farms that had less than 6000 hills per acre the potatoes were in check rows.

TABLE 67. Relation of Number of Hills per Acre to Production, Cost of Production, and Profit, 337 Farms, Steuben County, 1912

| Number of hills per acre | Number of farms | Average number of hills per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|
| 4,500–5,500 | 176 | 5,348 | 112 | $48.48 | $0.43 | $1.01 |
| 5,501–9,000 | 84 | 6,462 | 125 | 50.48 | 0.40 | 3.06 |
| Over 9,000 | 77 | 10,456 | 135 | 56.14 | 0.42 | 4.15 |

On farms having more than 6000 hills per acre the potatoes were in drills. Potatoes in drills required more horse hours and about the same

| Cost per bushel (cents) | Depth planted (inches) 1.1–2 | 2.1–3 | 3.1–4 | 4.1–5 | 5.1–6 | Totals |
|---|---|---|---|---|---|---|
| 16– 20 | | 1 | | 1 | | 2 |
| 21– 25 | 3 | 3 | 4 | | | 10 |
| 26– 30 | 6 | 11 | 6 | 1 | 1 | 25 |
| 31– 35 | 3 | 29 | 12 | 2 | | 46 |
| 36– 40 | 9 | 29 | 11 | 2 | | 51 |
| 41– 45 | 9 | 36 | 16 | 1 | | 62 |
| 46– 50 | 7 | 16 | 13 | 1 | | 37 |
| 51– 55 | 6 | 14 | 14 | 2 | | 36 |
| 56– 60 | 7 | 13 | 5 | 2 | 1 | 28 |
| 61– 65 | 2 | 7 | 8 | | | 17 |
| 66– 70 | 2 | 4 | 4 | | | 10 |
| 71– 75 | 3 | 5 | 2 | | | 10 |
| 76– 80 | | 2 | 2 | 1 | | 5 |
| 81– 85 | 1 | 2 | 1 | | | 4 |
| 86– 90 | | 1 | | 1 | | 2 |
| 91– 95 | 1 | 1 | 1 | | | 3 |
| 96–100 | | 1 | | | | 1 |
| 101–105 | | 1 | | | | 1 |
| 106–110 | | | | | | |
| 111–115 | | 1 | | | | 1 |
| 116–120 | | 1 | | | | 1 |
| 121–125 | | | | | | |
| 126–130 | | | | | | |
| 131–135 | | | | | | |
| 136–140 | | | | | | |
| 141–145 | | 1 | | | | 1 |
| 146–150 | | | | | | |
| 151–155 | | 1 | | | | 1 |
| 156–160 | | | | | | |
| 161–165 | | | | | | |
| 166–170 | | | 1 | | | 1 |
| Totals | 59 | 180 | 100 | 14 | 2 | 355 |

$r = 0.001 \pm 0.036$

FIG. 95. CORRELATION BETWEEN DEPTH OF PLANTING AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

number of man hours per acre as potatoes in check rows (table 68). This indicates a more extensive use of two-horse machinery on drilled potatoes. To some extent the number of bushels of seed used per

TABLE 68. Relation of Number of Hills per Acre to Factors Influencing Production and Cost of Production, 337 Farms, Steuben County, 1912

| Number of hills per acre | Man hours per acre | Horse hours per acre | Cost of fertilizer per acre | Cost of manure per acre | Bushels of seed per acre | Cost of seed per acre |
|---|---|---|---|---|---|---|
| 4,500–5,500..... | 79.3 | 81.9 | $1.01 | $4.48 | 9.2 | $ 8.65 |
| 5,501–9,000..... | 77.2 | 85.0 | 1.11 | 5.52 | 9.8 | 9.14 |
| Over 9,000..... | 80.5 | 89.5 | 3.34 | 4.72 | 12.2 | 11.50 |

acre is correlated with the number of hills per acre. The amount of seed used per plant was considerably lower on the farms having the most hills per acre than on those with the least hills per acre.

*Correlation between number of hills per acre and cost of potatoes per bushel.*— The coefficient of correlation between number of hills per acre and cost of potatoes per bushel was $-0.057 \pm 0.037$. The correlation is too small to warrant any conclusion. The distribution of farms is shown in the correlation chart (fig. 96).

### *Amount of seed used per acre*

If too little seed is used the yield per acre of potatoes may be limited. In Steuben County the best results were obtained when from 1.2 to 2 bushels of seed were planted per 1000 hills (tables 69 and 70). The use

TABLE 69. Relation of Amount of Seed Used per Acre to Production, Cost of Production, and Profit, 337 Farms, Steuben County, 1912

| Number of hills per acre | Bushels of seed per acre | Number of farms | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|
| 4,500–5,500 | 9 or less | 95 | 13.7 | 108 | $46.34 | $0.43 | $ 1.08 |
| | 9.1–11 | 68 | 15.0 | 116 | 49.63 | 0.43 | 2.90 |
| | 11.1–14 | 11 | 13.4 | 111 | 56.15 | 0.51 | — 9.65 |
| | Over 14 | 2 | 13.0 | 128 | 66.50 | 0.52 | — 15.42 |
| 5,501–9,000 | 9 or less | 27 | 13.3 | 114 | $46.48 | $0.41 | $4.00 |
| | 9.1–11 | 43 | 15.2 | 126 | 51.04 | 0.41 | 1.29 |
| | 11.1–14 | 13 | 13.7 | 138 | 55.57 | 0.40 | 7.14 |
| | Over 14 | 1 | 17.0 | 179 | 59.88 | 0.33 | 9.06 |
| Over 9,000 | 9 or less | 5 | 10.5 | 94 | $52.71 | $0.56 | —$11.24 |
| | 9.1–11 | 21 | 14.8 | 126 | 53.35 | 0.42 | 2.85 |
| | 11.1–14 | 37 | 19.0 | 131 | 55.69 | 0.42 | 3.79 |
| | Over 14 | 14 | 13.8 | 172 | 63.19 | 0.37 | 11.74 |

of more seed than this was wasteful. An increase in the amount of seed used per acre was usually accompanied by an increase in the number of hills per acre.

| Cost per bushel (cents) | Number of hills per acre | | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4,001– 5,000 | 5,001– 6,000 | 6,001– 7,000 | 7,001– 8,000 | 8,001– 9,000 | 9,001–10,000 | 10,001–11,000 | 11,001–12,000 | 12,001–13,000 | 13,001–14,000 | 14,001–15,000 | |
| 16– 20 | | 1 | | | | | 1 | | | | | 2 |
| 21– 25 | | 4 | 2 | | | | | 1 | | 2 | | 9 |
| 26– 30 | 2 | 12 | 2 | 2 | 1 | | 2 | | | | 1 | 22 |
| 31– 35 | 3 | 26 | 4 | 2 | 2 | 2 | 5 | | | | | 44 |
| 36– 40 | 4 | 20 | 8 | 2 | 2 | 4 | 7 | | | 1 | | 48 |
| 41– 45 | 2 | 30 | 7 | 2 | | 6 | 11 | 1 | | | | 59 |
| 46– 50 | 1 | 19 | 5 | | 2 | 2 | 6 | | | | | 35 |
| 51– 55 | 5 | 20 | 2 | | | 2 | 5 | 1 | | | | 35 |
| 56– 60 | 1 | 19 | 4 | | | 2 | 2 | | | | | 28 |
| 61– 65 | | 10 | 3 | | 1 | | 2 | | 1 | | | 17 |
| 66– 70 | 2 | 3 | 2 | | | 2 | | | | | | 9 |
| 71– 75 | | 4 | 1 | | | 1 | 3 | | | | | 9 |
| 76– 80 | 2 | 2 | 1 | | | | | | | | | 5 |
| 81– 85 | | 1 | 1 | | | | 1 | | | | | 3 |
| 86– 90 | | | 1 | 1 | | | | | | | | 2 |
| 91– 95 | 1 | 1 | | | | 1 | | | | | | 3 |
| 96–100 | | 1 | | | | | | | | | | 1 |
| 101–105 | | 1 | | | | | | | | | | 1 |
| 106–110 | | | | | | | | | | | | |
| 111–115 | | 1 | | | | | | | | | | 1 |
| 116–120 | | 1 | | | | | | | | | | 1 |
| 121–125 | | | | | | | | | | | | |
| 126–130 | | | | | | | | | | | | |
| 131–135 | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | |
| 141–145 | | 1 | | | | | | | | | | 1 |
| 146–150 | | | | | | | | | | | | |
| 151–155 | | | | | | | 1 | | | | | 1 |
| 156–160 | | | | | | | | | | | | |
| 161–165 | | | | | | | | | | | | |
| 166–170 | | 1 | | | | | | | | | | 1 |
| Totals | 23 | 178 | 43 | 9 | 8 | 22 | 46 | 3 | 1 | 3 | 1 | 337 |

$r = -0.057 \pm 0.037$

FIG. 96. CORRELATION BETWEEN NUMBER OF HILLS PER ACRE AND COST OF POTATOES PER BUSHEL, 337 FARMS, STEUBEN COUNTY, 1912

When the farms were divided into groups of approximately the same number of hills per acre, it appeared that an increase in the amount of seed used brought an increase in yield. The cost per bushel of crop was

FIG. 97. EFFECT OF SEED UPON STAND OF POTATOES IN STEUBEN COUNTY
Care should be taken to procure good seed

reduced by an increase of seed up to about 2 bushels per 1000 hills. There was a small increase in yield when more than 2 bushels of seed was planted

TABLE 70. RELATION OF AMOUNT OF SEED USED PER ACRE TO FACTORS INFLUENCING PRODUCTION, 337 FARMS, STEUBEN COUNTY, 1912

| Number of hills per acre | Bushels of seed per acre | Average bushels of seed per acre | Cost of seed per acre | Number of hills per acre | Bushels of seed per 1,000 hills |
|---|---|---|---|---|---|
| 4,500–5,500 | 9 or less | 8.1 | $ 7.47 | 5,337 | 1.5 |
| | 9.1–11 | 10.0 | 9.36 | 5,366 | 1.9 |
| | 11.1–14 | 12.1 | 12.76 | 5,373 | 2.2 |
| | Over 14 | 14.2 | 16.54 | 5,133 | 2.8 |
| 5,501–9,000 | 9 or less | 8.1 | $ 7.40 | 6,228 | 1.3 |
| | 9.1–11 | 10.0 | 9.16 | 6,293 | 1.6 |
| | 11.1–14 | 12.1 | 12.06 | 7,029 | 1.7 |
| | Over 14 | 14.7 | 14.71 | 8,386 | 1.8 |
| Over 9,000 | 9 or less | 8.6 | $ 7.71 | 9,589 | 0.9 |
| | 9.1–11 | 10.3 | 9.43 | 10,101 | 1.0 |
| | 11.1–14 | 12.5 | 11.47 | 10,409 | 1.2 |
| | Over 14 | 15.6 | 15.98 | 11,421 | 1.4 |

per 1000 hills, but this increase in yield was produced at a loss. Where less than 1 bushel of seed was used per 1000 hills there was a material reduction in yield.

*Method of planting*

In Steuben County there was a great difference in yield between hand-planted and machine-planted fields, as is shown in table 71. A large

TABLE 71. RELATION OF METHOD OF PLANTING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 350 FARMS, STEUBEN COUNTY, 1912

| Method of planting | Number of farms | Depth of planting (inches) | Acres in potatoes | Man hours per acre planting | Horse hours per acre planting | Cost per acre for use of planter | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| By hand..... | 280 | 3.1 | 13.8 | 7.6 | 6.8 | $0.00 | 115 | $49.52 | $0.43 | $0.88 |
| By automatic planter.. | 27 | 3.0 | 18.3 | 2.9 | 5.3 | 0.41 | 130 | 53.67 | 0.41 | 6.71 |
| By platform planter... | 43 | 3.0 | 18.6 | 4.9 | 5.0 | 0.48 | 147 | 57.21 | 0.39 | 7.54 |

part of this difference was due to a difference in the number of hills per acre. The potatoes planted by hand were usually planted in check rows,

FIG. 98. PLANTING POTATOES WITH AN AUTOMATIC, OR PICKER, PLANTER

while those planted with a planter were close together in the row and thus there were more hills per acre. The potatoes planted with a planter had less hills out of the row. This reduced the injury in cultivation. The difference in yield resulting from planting by the automatic, or picker, planter, and the platform, or two-man, planter, was probably due to a difference in stand. The platform planter required an extra man, but careful work by that man would reduce the number of skipped hills to a

FIG. 99. PLANTING POTATOES WITH A TWO-MAN, OR PLAFTORM, PLANTER

minimum. The cost for use of the planter was 41 cents per acre for an automatic planter and 48 cents per acre for a platform planter. This includes depreciation, repairs, and 10 per cent of the value of the planter to cover interest, housing, oil, and other costs.

*Cultivation practices*

The cultivation of potatoes in Steuben County included four operations which were usually performed in the following order: recovering, weeding, cultivating, and hilling. The number of farms following different combinations of operations is given in table 72:

TABLE 72. CULTIVATION PRACTICES, 355 FARMS, STEUBEN COUNTY, 1912

| Practice | Number of farms |
|---|---|
| Recovered – weeded – cultivated – hilled | 133 |
| Recovered – weeded – cultivated | 11 |
| Recovered - cultivated – hilled | 95 |
| Recovered – weeded - hilled | 1 |
| Recovered – hilled | 2 |
| Weeded – cultivated – hilled | 70 |
| Weeded – cultivated | 8 |
| Cultivated – hilled | 32 |
| Cultivated | 3 |

*Recovering*

Recovering was done on 242 of the 355 farms studied in Steuben County. This is an early-season operation, done when just enough of the potatoes are up to show the rows. The implement used is the potato hiller, which scrapes the dirt from between the rows to the rows, thus covering the small weeds and delaying their appearance above ground. The next cultivation, usually done with a weeder or a plank, levels off the ridge and exposes the small weeds, thus killing them.

The operation of recovering required an average of 2 man hours and 4 horse hours per acre. The farmers who recovered their potatoes received an average yield of 124 bushels per acre, while those who did not recover received 117 bushels per acre (table 73). The profit on the

TABLE 73. RELATION OF RECOVERING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| | Number of times over | Number of farms | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| Crop not recovered | 0 | 113 | 15.1 | 117 | $49.86 | $0.43 | $1.91 |
| Crop recovered | 1 | 242 | 14.5 | 124 | 51.73 | 0.42 | 2.74 |

farms where recovering was done was 83 cents per acre greater than on the farms where the potatoes were not recovered.

### *Weeding*

Weeding or planking was done on 223 of the 355 farms studied in Steuben County. Weeding and planking are grouped together because of their similarity in purpose and effect. The purpose of either operation is to scratch or scrape the surface of the soil, leveling it and exposing any weeds that may have germinated. It is an early-season operation preceding cultivation.

The relation of weeding to production, cost of production, and profit is shown in table 74. The number of times that the potatoes were weeded seemed to have little if any effect on the yield.

TABLE 74. Relation of Weeding to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Number of times weeded | Number of farms | Average number of times weeded | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| None | 132 | 0.0 | 12.9 | 122 | $50.04 | $0.41 | $2.94 |
| 0.1–1 | 109 | 0.8 | 15.6 | 117 | 48.96 | 0.42 | 3.69 |
| Over 1 | 114 | 2.2 | 15.9 | 126 | 54.17 | 0.43 | 0.88 |

*Correlation between number of times weeded and cost of potatoes per bushel.*— The coefficient of correlation between the number of times weeded and the cost of potatoes per bushel was $0.175 \pm 0.035$. The distribution of farms is shown in the correlation chart (fig. 100).

### *Cultivating*

Cultivating was done on 352 of the 355 farms studied in Steuben County. This is a midseason operation, usually begun as soon as the potato rows can be seen and continued until the vegetative growth is nearly completed.

Potatoes were planted in check rows on 254 of the 355 farms studied. The check rows were usually cultivated both ways. By this practice more ground was stirred by the cultivator, which made this method of planting more advantageous in weed control.

Cultivating seemed to be a profitable operation in Steuben County. There was a marked increase in yield as the number of cultivations was

| Cost per bushel (cents) | Number of times weeded: 0 | 0.1–1 | 1.1–2 | 2.1–3 | 3.1–4 | 4.1–5 | Totals |
|---|---|---|---|---|---|---|---|
| 16– 20 | | 2 | | | | | 2 |
| 21– 25 | 5 | 5 | | | | | 10 |
| 26– 30 | 12 | 3 | 6 | 4 | | | 25 |
| 31– 35 | 22 | 10 | 10 | 4 | | | 46 |
| 36– 40 | 18 | 15 | 12 | 4 | 2 | | 51 |
| 41– 45 | 20 | 22 | 14 | 3 | 3 | | 62 |
| 46– 50 | 15 | 10 | 10 | 2 | | | 37 |
| 51– 55 | 8 | 13 | 13 | 2 | | | 36 |
| 56– 60 | 11 | 10 | 3 | 3 | | 1 | 28 |
| 61– 65 | 8 | 6 | 3 | | | | 17 |
| 66– 70 | 4 | 4 | 2 | | | | 10 |
| 71– 75 | | 3 | 6 | 1 | | | 10 |
| 76– 80 | 1 | 3 | 1 | | | | 5 |
| 81– 85 | 1 | | 3 | | | | 4 |
| 86– 90 | 1 | 1 | | | | | 2 |
| 91– 95 | 2 | | | 1 | | | 3 |
| 96–100 | | 1 | | | | | 1 |
| 101–105 | | 1 | | | | | 1 |
| 106–110 | | | | | | | |
| 111–115 | 1 | | | | | | 1 |
| 116–120 | | | 1 | | | | 1 |
| 121–125 | | | | | | | |
| 126–130 | | | | | | | |
| 131–135 | | | | | | | |
| 136–140 | | | | | | | |
| 141–145 | 1 | | | | | | 1 |
| 146–150 | | | | | | | |
| 151–155 | 1 | | | | | | 1 |
| 156–160 | | | | | | | |
| 161–165 | | | | | | | |
| 166–170 | 1 | | | | | | 1 |
| Totals | 132 | 109 | 84 | 24 | 5 | 1 | 355 |

$r = 0.175 \pm 0.035$

FIG. 100. CORRELATION BETWEEN NUMBER OF TIMES WEEDED AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

increased, as is shown in table 75. Altho the profit did not increase steadily, there was an increase of $5.14 in profit on the farms that cultivated over 6 times as compared with the farms that cultivated 3 or less

TABLE 75. Relation of Cultivating to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Number of times cultivated | Number of farms | Average number of times cultivated | Number of times hilled | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| 3 or less | 144 | 2.6 | 2.2 | 14.4 | 115 | $48.24 | $0.42 | $1.87 |
| 3.1–5 | 161 | 4.3 | 1.9 | 14.2 | 118 | 51.28 | 0.43 | 0.99 |
| 5.1–6 | 25 | 6.0 | 1.7 | 17.4 | 146 | 56.53 | 0.39 | 8.78 |
| Over 6 | 25 | 7.9 | 1.1 | 16.6 | 149 | 59.07 | 0.40 | 7.01 |

times. The highest profit was on farms cultivating from 5.1 to 6 times. This profit was higher than normal, probably because of the larger acreage in potatoes on those farms. The farmers who cultivated the most hilled their potatoes the least.

*Correlation between number of times cultivated and cost of potatoes per bushel.*— The coefficient of correlation between the number of times cultivated and the cost of potatoes per bushel was $0.054 \pm 0.036$. As the probable error nearly equals the coefficient, little correlation is shown. The distribution of farms is given in the correlation chart (fig. 101).

### *Hilling*

Hilling or shovel plowing was done on 333 of the 355 farms studied in Steuben County. This was the last tillage operation. The primary reason for hilling in Steuben County was to leave the land in such a condition that the potatoes could be easily dug.

Hilling potatoes in Steuben County materially decreased the yield. On farms where the potatoes were not hilled, the average yield per acre was 156 bushels (table 76). On farms hilling over 2 times, the average

TABLE 76. Relation of Hilling to Production, Cost of Production, and Profit, 355 Farms, Steuben County, 1912

| Number of times hilled | Number of farms | Average number of times hilled | Number of times cultivated | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|
| None | 22 | 0.0 | 5.9 | 14.1 | 156 | $55.42 | $0.36 | $12.97 |
| 0.1–1 | 82 | 1.0 | 4.6 | 15.2 | 130 | 53.33 | 0.41 | 5.73 |
| 1.1–2 | 169 | 2.0 | 3.7 | 15.7 | 115 | 49.81 | 0.43 | — 0.09 |
| Over 2 | 82 | 3.3 | 3.6 | 15.2 | 116 | 50.24 | 0.43 | 1.19 |

yield per acre was 116 bushels. The probable reason for this decrease is that hilling is a deep cultivation and cuts off many of the potato roots

Number of times cultivated

| Cost per bushel (cents) | 0 | 0.1–1 | 1.1–2 | 2.1–3 | 3.1–4 | 4.1–5 | 5.1–6 | 6.1–7 | 7.1–8 | 8.1–9 | 9.1–10 | 10.1–11 | 11.1–12 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | | | | | 1 | | 1 | | | | | | | 2 |
| 21– 25 | | | 2 | 3 | | 4 | | 1 | | | | | | 10 |
| 26– 30 | | 1 | 4 | 6 | 5 | 2 | 4 | | 1 | 1 | | 1 | | 25 |
| 31– 35 | 1 | 2 | 6 | 13 | 14 | 4 | 2 | 1 | 3 | | | | | 46 |
| 36– 40 | | | 7 | 12 | 16 | 9 | 4 | 1 | 1 | 1 | | | | 51 |
| 41– 45 | | 1 | 6 | 18 | 24 | 5 | 4 | | 3 | | | | 1 | 62 |
| 46– 50 | | | 5 | 7 | 15 | 5 | 4 | 1 | | | | | | 37 |
| 51– 55 | | | 2 | 12 | 12 | 6 | 1 | 2 | | | 1 | | | 36 |
| 56– 60 | | 1 | 4 | 10 | 5 | 3 | 1 | 2 | 2 | | | | | 28 |
| 61– 65 | 1 | | | 6 | 4 | 4 | 2 | | | | | | | 17 |
| 66– 70 | 1 | | | 1 | 4 | 2 | 1 | 1 | | | | | | 10 |
| 71– 75 | | | | 2 | 5 | 1 | 1 | 1 | | | | | | 10 |
| 76– 80 | | | 1 | 2 | 2 | | | | | | | | | 5 |
| 81– 85 | | | 1 | 1 | 1 | 1 | | | | | | | | 4 |
| 86– 90 | | | | 1 | 1 | | | | | | | | | 2 |
| 91– 95 | | 1 | | | 2 | | | | | | | | | 3 |
| 96–100 | | | | | 1 | | | | | | | | | 1 |
| 101–105 | | | | 1 | | | | | | | | | | 1 |
| 106–110 | | | | | | | | | | | | | | |
| 111–115 | | | | | 1 | | | | | | | | | 1 |
| 116–120 | | | | 1 | | | | | | | | | | 1 |
| 121–125 | | | | | | | | | | | | | | |
| 126–130 | | | | | | | | | | | | | | |
| 131–135 | | | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | | | |
| 141–145 | | 1 | | | | | | | | | | | | 1 |
| 146–150 | | | | | | | | | | | | | | |
| 151–155 | | | | | 1 | | | | | | | | | 1 |
| 156–160 | | | | | | | | | | | | | | |
| 161–165 | | | | | | | | | | | | | | |
| 166–170 | | | | | | 1 | | | | | | | | 1 |
| Totals | 3 | 7 | 38 | 96 | 114 | 47 | 25 | 10 | 10 | 2 | 1 | 1 | 1 | 355 |

$r = 0.054 \pm 0.036$

FIG. 101. CORRELATION BETWEEN NUMBER OF TIMES CULTIVATED AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

in the upper layer of the soil. The scraping of the soil from between the rows allows the soil to become dry, thus killing the roots in the layer of soil below those cut off by the hiller. The farmers who did not hill made the greatest profit.

*Correlation between number of times hilled and cost of potatoes per bushel.*— The coefficient of correlation between the number of times hilled and the cost of potatoes per bushel was $0.070 \pm 0.036$. The distribution of farms is shown in the correlation chart (fig. 102).

| Cost per bushel (cents) | Number of times hilled: 0 | 0.1–1 | 1.1–2 | 2.1–3 | 3.1–4 | 4.1–5 | 5.1–6 | 6.1–7 | Totals |
|---|---|---|---|---|---|---|---|---|---|
| 16– 20 | 1 | | | 1 | | | | | 2 |
| 21– 25 | 2 | 3 | 4 | 1 | | | | | 10 |
| 26– 30 | 4 | 7 | 11 | 3 | | | | | 25 |
| 31– 35 | 3 | 9 | 26 | 4 | 3 | | | 1 | 46 |
| 36– 40 | 4 | 14 | 19 | 11 | 3 | | | | 51 |
| 41– 45 | 1 | 16 | 30 | 10 | 5 | | | | 62 |
| 46– 50 | | 10 | 20 | 6 | 1 | | | | 37 |
| 51– 55 | 1 | 4 | 18 | 7 | 6 | | | | 36 |
| 56– 60 | 3 | 8 | 14 | 1 | | 2 | | | 28 |
| 61– 65 | | 5 | 5 | 6 | 1 | | | | 17 |
| 66– 70 | 1 | 2 | 5 | 1 | 1 | | | | 10 |
| 71– 75 | | 1 | 7 | 2 | | | | | 10 |
| 76– 80 | 1 | | 1 | 2 | 1 | | | | 5 |
| 81– 85 | 1 | | 1 | 2 | | | | | 4 |
| 86– 90 | | | 2 | | | | | | 2 |
| 91– 95 | | | 2 | | 1 | | | | 3 |
| 96–100 | | 1 | | | | | | | 1 |
| 101–105 | | | 1 | | | | | | 1 |
| 106–110 | | | | | | | | | |
| 111–115 | | | 1 | | | | | | 1 |
| 116–120 | | | 1 | | | | | | 1 |
| 121–125 | | | | | | | | | |
| 126–130 | | | | | | | | | |
| 131–135 | | | | | | | | | |
| 136–140 | | | | | | | | | |
| 141–145 | | 1 | | | | | | | 1 |
| 146–150 | | | | | | | | | |
| 151–155 | | 1 | | | | | | | 1 |
| 156–160 | | | | | | | | | |
| 161–165 | | | | | | | | | |
| 166–170 | | | 1 | | | | | | 1 |
| Totals | 22 | 82 | 169 | 57 | 22 | 2 | | 1 | 355 |

$r = 0.070 \pm 0.036$

FIG. 102. CORRELATION BETWEEN NUMBER OF TIMES HILLED AND COST OF POTATOES PER BUSHEL, 355 FARMS, STEUBEN COUNTY, 1912

*Spraying with bordeaux*

On only 17 of the farms studied in Steuben County were the potatoes sprayed with bordeaux. The farmers who sprayed had larger yields and made better profits than those who did not spray, as is shown in table 77:

TABLE 77. RELATION OF SPRAYING WITH BORDEAUX TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| | Number of farms | Acres in potatoes | Cost of fertilizer per acre | Cost of manure per acre | Cost of fungicide per acre | Cost of insecticide per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| Sprayed with bordeaux | 17 | 21.2 | $3.78 | $3.64 | $1.09 | $0.35 | 142 | $58.71 | $0.41 | $5.05 |
| Not sprayed with bordeaux | 338 | 14.4 | 1.50 | 4.88 | 0.00 | 0.11 | 120 | 50.56 | 0.42 | 2.28 |
| Selected farms not sprayed with bordeaux | 32 | 18.8 | 3.49 | 4.61 | 0.00 | 0.13 | 143 | 54.39 | 0.38 | 9.76 |

However, the farmers who did not spray had smaller acreages of potatoes per farm and used less fertilizer than did the farmers who sprayed, and, as is shown in table 78, did not plow so deep.

TABLE 78. RELATION OF SPRAYING WITH BORDEAUX TO FACTORS INFLUENCING PRODUCTION, COST OF PRODUCTION, AND PROFIT, 355 FARMS, STEUBEN COUNTY, 1912

| | Number of farms | Elevation (feet) | Value of land per acre | Number of hills per acre | Depth of plowing (inches) | Miles to market |
|---|---|---|---|---|---|---|
| Sprayed with bordeaux | 17 | 1,664 | $47 | 7,781 | 7.1 | 3.1 |
| Not sprayed with bordeaux | 338 | 1,658 | 53 | ..... | 6.5 | 3.3 |
| Selected farms not sprayed with bordeaux | 32 | 1,707 | 55 | 7,856 | 7.0 | 3.5 |

To make a fairer comparison of the farms that sprayed and those that did not spray, 32 farms were selected which were nearly equal in all factors affecting potato production except spraying with bordeaux (table 77). On these 32 farms the average yield per acre was 143 bushels, produced at a cost of 38 cents per bushel. On the 17 farms that sprayed with bordeaux the average yield per acre was 142 bushels, produced at a

cost of 41 cents per bushel. Evidently, therefore, little benefit was derived from spraying with bordeaux in Steuben County in 1912. The fact that 41 of the 355 farmers owned traction sprayers but only 15 of these sprayers were used for spraying with bordeaux, suggests that past experience had not proved the use of bordeaux profitable in that region.

The cost of spraying 3.2 times with bordeaux on 17 farms in Steuben County was $2.87 per acre, or 90 cents for each time sprayed (table 79). This does not include a cost for insecticide of 35 cents per acre, or 11 cents for each time sprayed.

TABLE 79. Cost of Spraying 3.2 Times with Bordeaux, 17 Farms, Steuben County, 1912

| | Average cost per acre (for spraying 3.2 times) | Average cost per spraying |
|---|---|---|
| Fungicide | $1.09 | $0.34 |
| Man labor, 2.8 hours | 0.49 | 0.15 |
| Horse labor, 5.1 hours | 0.76 | 0.24 |
| Use of sprayer* | 0.53 | 0.17 |
| Total | $2.87 | $0.90 |

* The charge for use of sprayer includes depreciation, repairs, and a charge of 10 per cent on the value of the sprayer to cover interest, housing, oil, and similar items.

## RELATION OF VARIOUS FACTORS TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, SUFFOLK AND NASSAU COUNTIES, 1912

### *Acreage in potatoes*

The average acreage in potatoes per farm in the Suffolk County area was 19.6 acres. Twenty-two per cent of the farms had 10 acres or less in potatoes, and 12 per cent grew over 30 acres. As in Steuben County, the acreage in potatoes per farm had no effect on yield. This is shown in table 80.

The cost per acre and per bushel averaged the highest on farms having from 5 to 10 acres in potatoes, and the lowest on farms with over 15 acres in potatoes. The average profit per acre increased from $11.18, on the

TABLE 80. RELATION OF ACREAGE IN POTATOES TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Acres in potatoes | Number of farms | Total acres in potatoes | Average acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| 5–10 | 35 | 314.2 | 9.0 | 151 | $92.29 | $0.61 | $11.18 |
| 10.1–15 | 42 | 546.5 | 13.0 | 157 | 90.98 | 0.58 | 14.34 |
| 15.1–30 | 64 | 1,422.5 | 22.2 | 160 | 83.41 | 0.52 | 30.95 |
| Over 30 | 20 | 866.5 | 43.3 | 156 | 83.10 | 0.53 | 29.36 |

farms with small potato acreage, up to $30.95, more than double, on the farms with from 15.1 to 30 acres in potatoes. On farms with over 30 acres in potatoes the average profit per acre was slightly lower — $29.36. This decrease of cost and increase of profit was the result primarily of greater economy of labor on the larger acreages. Approximately 20 per cent less labor on potatoes was required per acre on farms with over 15 acres in the crop, than on those with from 5 to 10 acres. The cost per acre of fertilizer, manure, and seed was a little less on the larger acreages, as is shown in table 81:

TABLE 81. RELATION OF ACREAGE IN POTATOES TO HOURS OF LABOR, COST OF FERTILIZER, MANURE, AND SEED, AND LAND RENTAL, 161 FARMS, SUFFOLK COUNTY, 1912

| Acres in potatoes | Man hours per acre | Horse hours per acre | Cost of fertilizer per acre | Cost of manure per acre | Cost of seed per acre | Cost of land rental per acre |
|---|---|---|---|---|---|---|
| 5–10 | 89.6 | 78.5 | $29.71 | $1.39 | $15.57 | $12.30 |
| 10.1–15 | 85.7 | 74.8 | 29.31 | 2.27 | 14.30 | 13.22 |
| 15.1–30 | 75.4 | 64.5 | 27.17 | 0.58 | 14.54 | 13.20 |
| Over 30 | 70.9 | 66.4 | 27.95 | 0.32 | 14.90 | 12.08 |

The average acreage in potatoes per farm in the Nassau County area was 35.8 acres. The acreage in potatoes seemed to have no effect on the labor cost, or on the total cost per acre as shown in table 82. Because of the small number of farms studied, no conclusions can be drawn.

TABLE 82. Relation of Acreage in Potatoes to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| Acres in potatoes | Number of farms | Total acres in potatoes | Average acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| 5–20 | 13 | 186.3 | 14.3 | 176 | $103.18 | $0.59 | $37.97 |
| 20.1–50 | 19 | 609.0 | 32.0 | 185 | 118.99 | 0.64 | 18.94 |
| Over 50 | 9 | 671.0 | 74.6 | 192 | 111.39 | 0.58 | 30.52 |

The farmers growing the larger acreages of potatoes were on more valuable land and used more fertilizer per acre than those growing smaller acreages, as is shown in table 83:

TABLE 83. Relation of Acreage in Potatoes to Hours of Labor, Cost of Fertilizer, Manure, and Seed, and Land Rental, 41 Farms, Nassau County, 1912

| Acres in potatoes | Man hours per acre | Horse hours per acre | Cost of fertilizer per acre | Cost of manure per acre | Cost of seed per acre | Cost of land rental per acre |
|---|---|---|---|---|---|---|
| 5–20 | 94.8 | 105.9 | $27.32 | $3.07 | $15.29 | $12.36 |
| 20.1–50 | 117.0 | 128.3 | 30.23 | 1.56 | 16.77 | 15.83 |
| Over 50 | 101.8 | 108.0 | 32.20 | 1.40 | 13.92 | 16.69 |

*Miles to market*

The cost of marketing the potatoes sold was 1.7 cents per bushel for farms located two miles or less from the railway station, and 2.9 cents per

TABLE 84. Relation of Miles to Market to Cost of Hauling to Market, Cost of Growing and Marketing, and Profit, 161 Farms, Suffolk County, 1912

| Miles to market | Number of farms | Average miles to market | Man hours hauling per acre | Horse hours hauling per acre | Yield per acre (bushels) | Cost of labor and equipment for hauling per bushel | Cost of growing and marketing per acre | Cost of growing and marketing per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 2 or 'ess | 99 | 1.2 | 5.0 | 8.7 | 159 | $0.017 | $89.93 | $0.57 | $18.92 |
| 2.1–4 | 51 | 3.0 | 6.0 | 11.7 | 158 | 0.023 | 80.28 | 0.51 | 36.66 |
| Over 4 | 11 | 5.2 | 6.7 | 14.2 | 148 | 0.029 | 79.86 | 0.54 | 23.28 |

bushel for farms located over four miles from the station (table 84). The farms farthest from market used less fertilizer and less manure (table 85). These farms grew the largest acreage per farm, and had the lowest cost of growing and marketing per acre.

TABLE 85. RELATION OF MILES TO MARKET TO COST OF FERTILIZER, MANURE, AND SEED, AND TO LAND RENTAL, 161 FARMS, SUFFOLK COUNTY, 1912

| Miles to market | Acres in potatoes | Cost of fertilizer per acre | Cost of manure per acre | Cost of seed per acre | Cost of land rental per acre |
|---|---|---|---|---|---|
| 2 or less | 17.4 | $30.52 | $1.40 | $16.01 | $12.09 |
| 2.1–4 | 22.0 | 25.14 | 0.30 | 12.93 | 13.85 |
| Over 4 | 27.6 | 24.32 | 0.10 | 13.78 | 13.02 |

*Manure*

Stable manure was much less used in Suffolk and Nassau Counties than in Steuben County. Little stock was kept, and consequently little manure was produced on the farms. City stable manure shipped in from Brooklyn and New York was expensive. Manure was applied to potato land on only 22 of the 161 farms in Suffolk County and on 13 of the 41 farms in Nassau County. Usually this was applied to a small part of the total acreage.

The application of manure in both Suffolk and Nassau Counties increased the yield per acre, as is shown in tables 86 and 87. In Suffolk County the increase in yield from applications of manure exceeding a cost of $8 per acre was not sufficient to warrant the extra expense. In

TABLE 86. RELATION OF THE USE OF MANURE TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Cost of application per acre | Number of farms | Acres in potatoes | Tons of manure per acre | Cost of manure per acre | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 0 (No manure applied) | 139 | 19.4 | 0.0 | $ 0.00 | $27.78 | 155 | $ 84.31 | $0.54 | $25.62 |
| $1–$8 | 14 | 23.8 | 1.6 | 1.98 | 28.17 | 172 | 86.42 | 0.50 | 31.41 |
| Over $8 | 8 | 15.2 | 14.1 | 17.35 | 32.64 | 179 | 109.84 | 0.61 | 10.46 |

Nassau County, where the average cost of manure was $5.06 per acre, the profit was increased by $4.41 per acre.

TABLE 87. Relation of the Use of Manure to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| | Number of farms | Acres in potatoes | Tons of manure per acre | Cost of manure per acre | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| No manure | 28 | 35.0 | 0.0 | $0.00 | $30.79 | 183 | $110.38 | $0.60 | $25.19 |
| Manure | 13 | 37.4 | 3.4 | 5.06 | 30.69 | 196 | 119.79 | 0.61 | 29.60 |

*Fertilizer*

Much larger amounts of fertilizer were applied per acre in Suffolk and Nassau Counties than in Steuben County. The smallest application was 1100 pounds per acre and the largest was 3000 pounds per acre. In Suffolk County an increase in the amount of fertilizer applied per acre resulted in an increased yield, as is shown in table 88. There was also a

TABLE 88. Relation of the Use of Fertilizer to Production, Cost of Production, and Profit, 161 Farms, Suffolk County, 1912

| Cost of application per acre | Number of farms | Acres in potatoes | Pounds of fertilizer per acre | Cost of fertilizer per acre | Cost of manure per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| $15–$25 | 52 | 22.5 | 1,540 | $22.65 | $0.10 | 150 | $ 77.79 | $0.52 | $34.58 |
| $25.01–$30 | 54 | 18.3 | 1,840 | 28.04 | 0.60 | 148 | 85.24 | 0.58 | 16.78 |
| $30.01–$35 | 41 | 18.6 | 2,040 | 32.06 | 2.08 | 166 | 93.10 | 0.56 | 18.85 |
| Over $35 | 14 | 16.3 | 2,660 | 41.83 | 2.10 | 210 | 101.08 | 0.48 | 41.00 |

reduction in the cost per bushel of potatoes produced and an increase in the profit per acre, if the group of farms using the least amount of fertilizer per acre is not considered. These farms produced potatoes at a cost of 52 cents per bushel and made a profit of $34.58 per acre. This profit was exceeded only by the farms applying over $35 worth of fertilizer per acre.

In Nassau County the use of different amounts of fertilizer seemed to have little effect on the yield, as is shown in table 89. The number of records, however, is too small for any definite conclusion to be drawn.

TABLE 89. RELATION OF THE USE OF FERTILIZER TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| Pounds of fertilizer per acre | Number of farms | Acres in potatoes | Average pounds of fertilizer per acre | Cost of fertilizer per acre | Cost of manure per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 1,100–1,500 | 10 | 21.2 | 1,400 | $22.78 | $2.67 | 195 | $112.01 | $0.58 | $41.65 |
| 1,600–1,900 | 8 | 41.2 | 1,800 | 29.48 | 1.64 | 179 | 108.64 | 0.61 | 20.56 |
| 2,000 | 23 | 40.2 | 2,000 | 33.04 | 1.46 | 188 | 115.47 | 0.61 | 25.40 |

*Depth of plowing*

Depth of plowing varied from 3 to 9 inches in Suffolk County and from 4.5 to 12 inches in Nassau County. As in Steuben County, the best yields were secured on the farms that plowed the deepest (tables 90 and 91). In Suffolk County the profit was greatest on farms that plowed

TABLE 90. RELATION OF DEPTH OF PLOWING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Depth of plowing (inches) | Number of farms | Average depth of plowing (inches) | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| 4 or less | 10 | 3.8 | 15.8 | 144 | $87.94 | $0.61 | $16.75 |
| 4.1–5 | 35 | 4.9 | 19.3 | 144 | 83.81 | 0.58 | 17.95 |
| 5.1–6 | 70 | 5.9 | 20.5 | 160 | 82.82 | 0.52 | 31.47 |
| 6.1–7 | 33 | 6.9 | 20.8 | 165 | 90.02 | 0.55 | 24.29 |
| Over 7 | 13 | 8.2 | 14.8 | 168 | 93.76 | 0.56 | 21.45 |

TABLE 91. RELATION OF DEPTH OF PLOWING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| Depth of plowing (inches) | Number of farms | Average depth of plowing (inches) | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|
| 4–6 | 16 | 5.7 | 39.2 | 174 | $112.24 | $0.65 | $14.18 |
| 6.1–8 | 18 | 7.7 | 34.6 | 193 | 113.10 | 0.59 | 31.34 |
| Over 8 | 7 | 9.7 | 30.9 | 209 | 118.35 | 0.57 | 49.44 |

from 5.1 to 6 inches deep. In Nassau County the farmers who plowed over 8 inches deep received the best profit.

In Suffolk County the cost of plowing over 7 inches deep, averaging 8.2 inches, was $2.69 per acre, while plowing 4 inches deep or less, averaging 3.8 inches, cost $2.47 (table 92). In Nassau County the cost of

TABLE 92. Relation of Depth of Plowing to Hours of Labor and Cost of Plowing, 161 Farms, Suffolk County, 1912

| Depth of plowing (inches) | Average depth of plowing (inches) | Man hours per acre plowing | Horse hours per acre plowing | Cost of labor and equipment per acre plowing |
|---|---|---|---|---|
| 4 or less | 3.8 | 4.3 | 8.6 | $2.47 |
| 4.1–5 | 4.9 | 3.7 | 8.3 | 2.31 |
| 5.1–6 | 5.9 | 3.8 | 8.7 | 2.40 |
| 6.1–7 | 6.9 | 3.9 | 8.7 | 2.42 |
| Over 7 | 8.2 | 4.5 | 9.5 | 2.69 |

plowing over 8 inches deep, averaging 9.7 inches, was $2.99 per acre, while plowing from 4 to 6 inches deep, averaging 5.7 inches, cost $2.61 (table 93). It is evident that deep plowing added materially to the yield without very much increase in cost.

TABLE 93. Relation of Depth of Plowing to Hours of Labor and Cost of Plowing, 41 Farms, Nassau County, 1912

| Depth of plowing (inches) | Average depth of plowing (inches) | Man hours per acre plowing | Horse hours per acre plowing | Cost of labor and equipment per acre plowing |
|---|---|---|---|---|
| 4–6 | 5.7 | 4.4 | 9.2 | $2.61 |
| 6.1–8 | 7.7 | 4.1 | 9.1 | 2.54 |
| Over 8 | 9.7 | 5.2 | 10.4 | 2.99 |

*Fitting*

Potato land was usually harrowed from 1 to 2 times in Suffolk and Nassau Counties. Only 23 of the 161 farmers in Suffolk County and

7 of the 41 farmers in Nassau County harrowed more than 2 times. Only 10 farmers rolled their potato land. The farmers in Suffolk County who harrowed the greatest number of times also plowed the deepest.

The farmers in Suffolk County who harrowed once raised their potatoes at a cost of $82.57 per acre, or 55 cents per bushel (table 94). The farmers

TABLE 94. RELATION OF NUMBER OF TIMES HARROWED TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Number of times harrowed | Number of farms | Average number of times harrowed | Depth of plowing (inches) | Acres in potatoes | Cost of fertilizer per acre | Cost of manure per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1..... | 67 | 1.0 | 5.8 | 21.2 | $27.77 | $0.71 | $14.38 | 149 | $82.57 | $0.55 | $22.05 |
| 2..... | 71 | 2.0 | 6.0 | 19.8 | 27.78 | 0.94 | 14.94 | 161 | 86.49 | 0.54 | 28.52 |
| Over 2.. | 23 | 3.6 | 6.4 | 14.1 | 30.03 | 1.39 | 15.06 | 182 | 94.27 | 0.52 | 29.08 |

who harrowed 3.6 times raised their potatoes at a cost of $94.27 per acre, or 52 cents per bushel. A part of their gain in yield is accounted for by the deeper plowing.

In Nassau County the farmers who harrowed 3 times or over raised their potatoes at a cost of $117.23 per acre, or 64 cents per bushel (table 95). Those who harrowed but once raised their potatoes at a cost of $111.85 per acre, or 60 cents per bushel. The farmers who harrowed

TABLE 95. RELATION OF NUMBER OF TIMES HARROWED TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| Number of times harrowed | Number of farms | Average number of times harrowed | Depth of plowing (inches) | Acres in potatoes | Cost of fertilizer per acre | Cost of manure per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1..... | 23 | 1.0 | 7.3 | 35.6 | $30.78 | $2.11 | $14.84 | 188 | $111.85 | $0.60 | $31.40 |
| 2..... | 11 | 2.0 | 7.2 | 38.2 | 31.36 | 1.17 | 14.68 | 187 | 114.70 | 0.61 | 20.65 |
| 3 or more | 7 | 3.1 | 7.1 | 32.6 | 29.60 | 1.04 | 17.95 | 184 | 117.23 | 0.64 | 20.69 |

once plowed the deepest. It is probable that for most farms on Long Island 1 or 2 harrowings would be as profitable as a larger number.

*Depth of planting*

The depth of planting potatoes had little effect on yield in Suffolk and Nassau Counties (tables 96 and 97). The results from Steuben, Suffolk,

TABLE 96. Relation of Depth of Planting to Production, Cost of Production, and Profit, 161 Farms, Suffolk County, 1912

| Depth of planting (inches) | Number of farms | Average depth of planting (inches) | Acres in potatoes | Cost of fertilizer per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 1–2 | 24 | 1.9 | 20.6 | $25.51 | $12.91 | 149 | $80.17 | $0.54 | $27.35 |
| 2.1–3 | 71 | 2.9 | 21.2 | 27.52 | 14.71 | 158 | 84.18 | 0.53 | 29.03 |
| 3.1–4 | 58 | 3.9 | 17.6 | 30.10 | 15.83 | 161 | 90.32 | 0.56 | 19.28 |
| Over 4 | 8 | 4.8 | 16.1 | 26.78 | 12.53 | 156 | 83.68 | 0.54 | 30.36 |

TABLE 97. Relation of Depth of Planting to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| Depth of planting (inches) | Number of farms | Average depth of planting (inches) | Acres in potatoes | Cost of fertilizer per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 7 | 2.0 | 28.1 | $28.54 | $17.45 | 195 | $120.94 | $0.62 | $35.73 |
| 2.1–3.9 | 16 | 3.1 | 44.6 | 31.08 | 13.70 | 184 | 109.49 | 0.60 | 27.43 |
| 4 or more | 18 | 4.4 | 30.9 | 31.12 | 16.53 | 189 | 116.04 | 0.61 | 22.45 |

and Nassau Counties seem to indicate that depth of planting is of minor importance in potato production.

### *Number of hills per acre*

In Suffolk County the best yield and the largest profit per acre was secured when from 12,001 to 15,000 hills were planted to the acre (table 98). This is equal to a variation in the distance between hills of from

TABLE 98. Relation of Number of Hills per Acre to Production, Cost of Production, and Profit, 157 Farms, Suffolk County, 1912

| Number of hills per acre | Number of farms | Cost of fertilizer per acre | Bushels of seed per acre | Bushels of seed per 1000 hills | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 9,000–12,000 | 64 | $25.55 | 11.4 | 1.02 | $13.36 | 146 | $80.45 | $0.55 | $25.37 |
| 12,001–15,000 | 71 | 28.43 | 12.3 | 0.87 | 15.36 | 172 | 88.75 | 0.52 | 32.24 |
| Over 15,000 | 22 | 34.70 | 12.5 | 0.72 | 16.96 | 148 | 91.63 | 0.62 | 5.11 |

12 to 16 inches when the rows are 34 inches apart. Over 15,000 hills per acre, or less than 12 inches apart in the row, was evidently more than could profitably be grown in 1912. Possibly more rainfall in June and

July would have been sufficient to make over 15,000 hills per acre the most profitable method of planting.

In Nassau County the best yield was secured by farmers planting the greatest number of hills per acre (table 99). These farmers, however,

TABLE 99. RELATION OF NUMBER OF HILLS PER ACRE TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| Number of hills per acre | Number of farms | Cost of fertilizer per acre | Bushels of seed per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| 12,000–16,000 | 22 | $29.83 | 12.3 | $16.11 | 176 | $107.53 | $0.61 | $27.80 |
| 16,001–18,000 | 13 | 31.98 | 12.8 | 15.12 | 190 | 118.87 | 0.62 | 25.27 |
| Over 18,000 | 6 | 31.23 | 12.0 | 12.96 | 214 | 121.62 | 0.57 | 25.82 |

received 8 cents less per bushel for their potatoes than did the farmers growing from 12,000 to 16,000 hills per acre. The farmers growing from 12,000 to 16,000 hills per acre made the largest profit on their potatoes. Those having over 18,000 hills per acre raised their potatoes at the lowest cost per bushel.

*Amount of seed used per acre*

The average value of the seed used for the 1912 crop of potatoes in Suffolk and Nassau Counties was $1.23 per bushel.

Farmers planting from 9000 to 12,000 hills per acre received the best yield and the greatest profit when from 10.1 to 12 bushels of seed per acre was used (table 100). In Nassau County the farmers using 12 or less

TABLE 100. RELATION OF AMOUNT OF SEED USED PER ACRE TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 157 FARMS, SUFFOLK COUNTY, 1912

| Number of hills per acre | Bushels of seed per acre | Number of farms | Acres in potatoes | Average bushels of seed per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|---|
| 9,000–12,000 | 10 or less | 19 | 19.4 | 9.7 | $11.75 | 138 | $78.78 | $0.57 | $21.04 |
| | 10.1–12 | 35 | 23.1 | 11.6 | 13.90 | 152 | 81.27 | 0.53 | 29.24 |
| | 12.1–14 | 6 | 21.8 | 12.8 | 12.97 | 132 | 77.78 | 0.59 | 18.48 |
| | Over 14 | 4 | 15.5 | 14.8 | 16.69 | 142 | 85.31 | 0.60 | 14.98 |
| 12,001–15,000 | 10 or less | 13 | 17.2 | 9.7 | $11.53 | 146 | $78.99 | $0.54 | $35.53 |
| | 10.1–12 | 31 | 15.3 | 11.3 | 14.13 | 169 | 85.94 | 0.51 | 27.11 |
| | 12.1–14 | 17 | 21.4 | 13.0 | 16.13 | 180 | 91.97 | 0.51 | 34.98 |
| | Over 14 | 10 | 30.2 | 14.9 | 19.18 | 188 | 96.52 | 0.51 | 34.56 |
| Over 15,00 | 10 or less | 0 | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| | 10.1–12 | 11 | 15.9 | 11.5 | $16.10 | 159 | $89.69 | $0.56 | $10.48 |
| | 12.1–14 | 10 | 22.2 | 13.1 | 17.20 | 136 | 92.12 | 0.68 | — 2.59 |
| | Over 14 | 1 | 20.0 | 14.5 | 21.85 | 190 | 103.10 | 0.54 | 43.80 |

bushels of seed produced their potatoes at the lowest cost per bushel and generally made the best profit (table 101).

TABLE 101. Relation of Amount of Seed Used per Acre to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| Number of hills per acre | Bushels of seed per acre | Number of farms | Acres in potatoes | Average bushels of seed per acre | Cost of seed per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| 12,000–16,000 | 12 or less... | 11 | 39.6 | 11.4 | $14.91 | 179 | $106.17 | $0.59 | $39.11 |
| | Over 12.... | 11 | 28.7 | 13.5 | 17.76 | 173 | 109.40 | 0.63 | 12.20 |
| 16,001–18,000 | 12 or less... | 5 | 45.6 | 11.0 | $12.85 | 182 | $109.23 | $0.60 | $24.18 |
| | Over 12.... | 8 | 31.1 | 14.4 | 17.20 | 198 | 127.70 | 0.64 | 26.27 |
| Over 18,000 | 12 or less... | 4 | 44.2 | 10.8 | $10.96 | 217 | $117.05 | $0.54 | $32.39 |
| | Over 12.... | 2 | 30.5 | 15.5 | 18.75 | 207 | 134.87 | 0.65 | 6.74 |

### *Method of planting*

The method of planting potatoes seemed to have little effect on the yield in Suffolk and Nassau Counties (tables 102 and 103). On Long

TABLE 102. Relation of Method of Planting to Production, Cost of Production, and Profit, 157 Farms, Suffolk County, 1912

| Method of planting | Number of farms | Depth of planting (inches) | Number of hills per acre | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| By automatic planter.... | 123 | 3.2 | 13,086 | 20.3 | 159 | $85.00 | $0.53 | $27.81 |
| By platform planter..... | 34 | 3.2 | 12,900 | 17.9 | 155 | 87.20 | 0.56 | 18.80 |

TABLE 103. Relation of Method of Planting to Production, Cost of Production, and Profit, 40 Farms, Nassau County, 1912

| Method of planting | Number of farms | Depth of planting (inches) | Number of hills per acre | Acres in potatoes | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| By automatic planter..... | 32 | 3.6 | 16,255 | 36.3 | 184 | $112.41 | $0.61 | $25.65 |
| By platform planter..... | 8 | 3.2 | 15,542 | 24.9 | 183 | 114.92 | 0.63 | 51.03 |

Island the average number of hills was much nearer to the point where a maximum yield would be obtained than was the case in Steuben County, and under such conditions a certain proportion of missing hills has less

effect on the yield. It is probable also that the automatic planter is more efficient on land that is level and without stones than on rougher ground.

The platform planter required on the average from 2.1 to 2.4 man hours per acre more than did the automatic planter (table 104). The requirement for horse labor was nearly the same. In Nassau County the

TABLE 104. TIME REQUIRED FOR PLANTING, AND COST OF PLANTER PER ACRE, 157 FARMS IN SUFFOLK COUNTY AND 40 FARMS IN NASSAU COUNTY, 1912

| Method of planting | Suffolk County | | | Nassau County | | |
|---|---|---|---|---|---|---|
| | Man hours per acre planting | Horse hours per acre planting | Cost per acre of use of planter | Man hours per acre planting | Horse hours per acre planting | Cost per acre of use of planter |
| By automatic planter | 3.0 | 5.4 | $0.48 | 3.0 | 5.8 | $0.43 |
| By platform planter | 5.1 | 5.4 | 0.49 | 5.4 | 5.5 | 0.61 |

cost of use of planter, including depreciation, repairs, and 10 per cent of the value for interest, housing, oil, and like costs, was 18 cents per acre higher for the platform planter than for the automatic planter.

### *Weeding*

In Suffolk County the farmers who weeded at least 2 times had the best yield and the largest profit per acre (table 105). The farmers who weeded more than 4 times gained nothing in yield.

TABLE 105. RELATION OF WEEDING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Number of times weeded | Number of farms | Average number of times weeded | Number of times hoed | Number of times cultivated | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|
| Less than 2 | 49 | 1.8 | 1.8 | 6.0 | $29.60 | 144 | $87.78 | $0.61 | $14.53 |
| 2–4 | 88 | 3.6 | 1.6 | 6.1 | 27.55 | 163 | 85.41 | 0.52 | 29.64 |
| Over 4 | 24 | 6.0 | 1.1 | 7.2 | 27.23 | 160 | 83.18 | 0.52 | 29.25 |

In Nassau County, as in Suffolk County, the farmers receiving the best yields weeded a medium number of times. The best results were obtained by weeding from 2 to 4 times (table 106).

TABLE 106. Relation of Weeding to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| Number of times weeded | Number of farms | Average number of times weeded | Number of times hoed | Number of times cultivated | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit or loss per acre |
|---|---|---|---|---|---|---|---|---|---|
| Less than 2..... | 6 | 1.6 | 0.8 | 3.5 | $31.23 | 142 | $108.11 | $0.76 | —$13.76 |
| 2–4..... | 26 | 3.6 | 0.5 | 3.5 | 31.07 | 205 | 113.04 | 0.55 | 40.66 |
| Over 4..... | 9 | 5.4 | 0.6 | 3.8 | 29.60 | 159 | 117.77 | 0.74 | 8.25 |

*Cultivating*

In Suffolk County the farmers who cultivated from 5 to 6 times had better yields and made larger profits than those who cultivated either a greater or a less number of times (table 107).

TABLE 107. Relation of Cultivating to Production, Cost of Production, and Profit, 161 Farms, Suffolk County, 1912

| Number of times cultivated | Number of farms | Average number of times cultivated | Number of times weeded | Number of times hilled | Number of times hoed | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| 4 or less..... | 21 | 3.8 | 3.0 | 0.7 | 1.7 | $30.81 | 157 | $89.79 | $0.57 | $18.10 |
| 5–6..... | 89 | 5.6 | 3.5 | 0.4 | 1.5 | 28.86 | 167 | 86.38 | 0.52 | 30.36 |
| 7 or over..... | 51 | 8.3 | 4.1 | 0.2 | 1.6 | 25.58 | 143 | 82.51 | 0.58 | 21.16 |

In Nassau County the farmers who cultivated from 3 times or less raised their potatoes at a cost of 59 cents per bushel and made a profit of $28.43 per acre, while the farmers who cultivated from 4 to 5 times raised their potatoes at a cost of 61 cents per bushel and made a profit of $28.06 per acre (table 108).

TABLE 108. Relation of Cultivating to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| Number of times cultivated | Number of farms | Average number of times cultivated | Number of times weeded | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| 3 or less..... | 18 | 2.7 | 3.6 | $31.60 | 190 | $112.78 | $0.59 | $28.43 |
| 4–5..... | 17 | 4.4 | 3.8 | 30.29 | 185 | 112.47 | 0.61 | 28.06 |
| Over 5..... | 6 | 6.7 | 4.4 | 26.72 | 178 | 121.36 | 0.68 | 10.90 |

### *Hilling*

Only 48 of the 161 Suffolk County farmers hilled their potatoes in 1912. The farmers who hilled the most harvested the largest yields and raised their crops at the lowest cost per bushel (table 109). These farmers also made the greatest profit per acre.

TABLE 109. RELATION OF HILLING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 161 FARMS, SUFFOLK COUNTY, 1912

| Number of times hilled | Number of farms | Average number of times hilled | Number of times weeded | Number of times hoed | Number of times cultivated | Value of land per acre | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|---|
| None | 113 | 0.0 | 3.6 | 1.5 | 6.3 | $242 | $27.91 | 150 | $84.77 | $0.57 | $21.33 |
| 0.1–1 | 31 | 0.9 | 3.9 | 1.8 | 6.7 | 242 | 25.74 | 155 | 83.37 | 0.54 | 28.30 |
| Over 1 | 17 | 2.0 | 3.4 | 1.2 | 5.1 | 333 | 34.52 | 220 | 96.50 | 0.44 | 50.58 |

In Nassau County the potatoes were hilled more than in Suffolk County but not so much as in Steuben County. The farmers who hilled the most in Nassau County had a yield greater by 14 bushels per acre than the farmers who did not hill (table 110). The cost of growing and marketing per bushel was the lowest on the farms where the most hilling was done.

TABLE 110. RELATION OF HILLING TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| Number of times hilled | Number of farms | Average number of times hilled | Number of times weeded | Number of times hoed | Number of times cultivated | Cost of fertilizer per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| None | 10 | 0 | 3.7 | 0.6 | 4.4 | $27.43 | 180 | $114.73 | $0.64 | $25.00 |
| 0.1–1.9 | 26 | 1 | 3.5 | 0.5 | 3.6 | 30.85 | 186 | 112.47 | 0.60 | 27.84 |
| 2 or more | 5 | 2 | 4.2 | 0.5 | 2.9 | 32.60 | 194 | 114.93 | 0.59 | 25.19 |

### *Hoeing*

In Suffolk County the potatoes that were hoed the most were on the cheapest land (table 111). The amount spent for manure and fertilizer on the farms that did not hoe was $28.34 per acre; on those that hoed from 0.5 to 1 time it was $30.70 per acre; and on the farms that hoed over 1 time it was $27.97 per acre. It is significant that farmers who

TABLE 111. Relation of Hoeing to Production, Cost of Production, and Profit 161 Farms, Suffolk County, 1912

| Number of times hoed | Number of farms | Average number of times hoed | Number of times weeded | Number of times cultivated | Number of times hilled | Value of land per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|---|---|
| None | 14 | 0.0 | 4.6 | 5.9 | 0.6 | $310 | 181 | $83.63 | $0.46 | $42.83 |
| 0.5–1 | 54 | 1.0 | 3.9 | 6.2 | 0.3 | 246 | 162 | 86.92 | 0.54 | 28.61 |
| Over 1 | 93 | 2.1 | 3.3 | 6.5 | 0.4 | 241 | 151 | 85.10 | 0.56 | 20.64 |

did not hoe their potatoes used weeders oftener than those who did hoe. They received the largest yield and made the greatest profit.

In Nassau County hoeing did not seem to affect the yield. The farmers who did not hoe, grew and marketed their potatoes at a cost of 58 cents per bushel, as compared with 63 cents per bushel for the farmers who hoed (table 112).

TABLE 112. Relation of Hoeing to Production, Cost of Production, and Profit, 41 Farms, Nassau County, 1912

| | Number of farms | Average number of times hoed | Number of times weeded | Number of times cultivated | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| Not hoed | 15 | 0.0 | 3.7 | 3.1 | 191 | $110.35 | $0.58 | $36.55 |
| Hoed | 26 | 0.9 | 3.7 | 3.9 | 184 | 115.84 | 0.63 | 19.35 |

### *Spraying with bordeaux*

Spraying with bordeaux gave a marked increase in yield in Suffolk County. The 114 farmers who did not spray had an average yield of 144 bushels of potatoes per acre (table 113). The 47 farmers who sprayed

TABLE 113. Relation of Spraying with Bordeaux to Production, Cost of Production, and Profit, 161 Farms, Suffolk County, 1912

| Number of times sprayed | Number of farms | Cost of fertilizer per acre | Cost of fungicide per acre | Cost of insecticide per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| None | 114 | $27.52 | $0.00 | $0.70 | 144 | $82.31 | $0.57 | $18.86 |
| 1–3 | 10 | 26.71 | 0.77 | 0.44 | 162 | 84.96 | 0.52 | 32.36 |
| 4–6 | 24 | 29.67 | 2.14 | 0.60 | 187 | 92.13 | 0.49 | 37.22 |
| Over 6 | 13 | 29.57 | 2.48 | 0.89 | 203 | 98.66 | 0.49 | 52.16 |

FIG. 103. SPRAYING POTATOES WITH BORDEAUX IN SUFFOLK COUNTY

had an average yield of 186 bushels per acre. Spraying over 6 times paid best in Suffolk County.

In Nassau County the farmers who did not spray used more fertilizer and hence there was little difference in yield (table 114). The farmers

TABLE 114. RELATION OF SPRAYING WITH BORDEAUX TO PRODUCTION, COST OF PRODUCTION, AND PROFIT, 41 FARMS, NASSAU COUNTY, 1912

| | Number of farms | Cost of fertilizer per acre | Cost of fungicide per acre | Cost of insecticide per acre | Yield per acre (bushels) | Cost per acre | Cost per bushel | Profit per acre |
|---|---|---|---|---|---|---|---|---|
| Not sprayed | 36 | $31.19 | $0.00 | $0.69 | 187 | $114.03 | $0.61 | $25.62 |
| Sprayed | 5 | 23.08 | 2.48 | 0.98 | 190 | 104.17 | 0.55 | 45.30 |

who sprayed raised their potatoes for 6 cents per bushel less than the farmers who did not spray. The profit per acre on the farms that sprayed was $19.68 more than on the farms that did not spray.

## SUGGESTED FORM OF SURVEY BLANK FOR POTATOES

Farm No..... Date.....19....

Operator..... P. O.....

Location.....Miles to shipping point.....Soil types.....

Acres farmed..... Elevation..... .....

Crop Production for 19....

| Crop | Acres | Yield per acre | Total |
|---|---|---|---|
| Corn, grain | | | |
| Corn, silage | | | |
| Corn, other | | | |
| Wheat | | | |
| Rye | | | |
| Oats | | | |
| Barley | | | |
| Buckwheat | | | |
| Hay | | | |
| Apples bearing | | | |
| Apples not bearing | | | |
| Potatoes | | | |
| Total crop acres | | | |

Potato Production

| Year | Varieties | Acres | Yield per acre | Total yield |
|---|---|---|---|---|
| 19 | | | | |
| | | | | |
| Total | | | | |

Potato Production (*concluded*)

| Year | Varieties | Acres | Yield per acre | Total yield |
|---|---|---|---|---|
| 19 | | | | |
| | | | | |
| | | | | |
| Total | | | | |
| 19 | | | | |
| | | | | |
| | | | | |
| Total | | | | |

Disposition of Crop

| | Bushels | Price per bushel | Total |
|---|---|---|---|
| Sold from field | | | |
| Sold from storage | | | |
| Seed | | | |
| Stock feed | | | |
| Used in house | | | |
| Waste | | | |
| Total | | | |

Expenses

| | Amount | Price per unit | Total |
|---|---|---|---|
| Land rental | | | |
| Fertilizer | | | |
| Manure | | | |
| Seed | | | |
| Bordeaux mixture (copper sulfate and lime) | | | |
| Insecticides | | | |
| Crates, baskets, barrels (average per year) | | | |
| Materials for treating seed | | | |
| Storage | | | |
| Man labor | | | |
| Horse labor | | | |
| Equipment | | | |
| Total | | | |

Labor

| | Date | Acres | Per acre | | Total | |
|---|---|---|---|---|---|---|
| | | | Man hours | Horse hours | Man hours | Horse hours |
| Growing | | | | | | |
| Plowing | | | | | | |
| Dragging, times | | | | | | |
| Disking, times | | | | | | |
| Rolling, times | | | | | | |
| Planting (machine) | | | | | | |
| Planting (hand) | | | | | | |
| Fertilizing | | | | | | |
| Hoeing, times | | | | | | |
| Recovering, times | | | | | | |
| Weeding, times | | | | | | |
| Planking, times | | | | | | |
| Cultivating, times | | | | | | |
| Hilling, times | | | | | | |
| Spraying, times | | | | | | |
| Digging (hand) | | | | | | |
| Digging (machine) | | | | | | |
| Picking up | | | | | | |
| Hauling to storage | | | | | | |
| Total growing | | | | | | |
| Marketing | | | | | | |
| Hauling to market | | | | | | |
| Sorting and bagging in storage | | | | | | |
| Hauling from storage to market | | | | | | |
| Total marketing | | | | | | |
| Growing and marketing | | | | | | |

Special Equipment

| Kind | Make | Value at beginning of year | Value at end of year | Repairs and upkeep | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Cash | Man labor | | Horse labor | |
| | | | | | Hours | Cost | Hours | Cost |
| Planter | | | | | | | | |
| Sprayer | | | | | | | | |
| Digger | | | | | | | | |

Manure

| | | | |
|---|---|---|---|
| Applied directly, ..... tons | $..... | ..... |
| Man labor, ..... hours | ..... | ..... |
| Horse and equipment labor, ..... hours | ..... | ..... |
| Total ..... | ..... | ....% |
| Applied preceding crop, ..... tons | ..... | ..... |
| Man labor, ..... hours | ..... | ..... |
| Horse and equipment labor, ..... hours | ..... | ..... |
| Total ..... | ..... | ....% |

Storag

| | | | |
|---|---|---|---|
| Value of potato buildings ..... | $..... | @.....% | $..... |
| Fuel ..... | ..... | ..... | ..... |
| Insurance ..... | ..... | ..... | ..... |
| Man labor, ..... hours | ..... | ..... | ..... |
| Horse and equipment labor, ..... hours | ..... | ..... | ..... |
| Cash paid for storage ..... | ..... | ..... | ..... |
| Total ..... | ..... | ..... | ..... |

General Questions

| | 19... | 19... | 19... |
|---|---|---|---|
| Bushels of crop stored ..... | ..... | ..... | ..... |
| Length of time stored ..... | ..... | ..... | ..... |
| Bushels wasted in storage ..... | ..... | ..... | ..... |
| Price at harvest time, per bushel ..... | ..... | ..... | ..... |
| Price received for stored potatoes ..... | ..... | ..... | ..... |
| ..... | ..... | ..... | ..... |
| ..... | ..... | ..... | ..... |

Value of farm (per acre, $.....) ..... $.....
Value of potato land per acre ..... $.....
Rental value of potato land per acre ..... $.....

Source of seed .....
Width of rows ..... Distance apart of rows .....
Crops preceding potatoes ..... 19..... 19..... 19..... 19.....
Surface (hilly, rolling, level) .....
Fertilizer analysis, N ..... $P_2O_5$ ..... $K_2O$ .....
Depth plowed ..... inches .....
Depth planted ..... inches .....
Crop on which manure is applied .....
Wages paid:— Wages per month..... year..... Board..... Total.....
Wages per month..... year..... Board..... Total.....
Day wages..... month..... Board..... Total.....

Summary
Receipts ..... $.....
Expenses ..... $.....
Profit ..... $.....

Memoir 20, *The Physiological Action of Nitrobenzene Vapor on Animals*, the second preceding number in this series of publications, was mailed on May 1, 1919.

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CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

# THE INHERITANCE OF THE WEAK AWN IN CERTAIN AVENA CROSSES AND ITS RELATION TO OTHER CHARACTERS OF THE OAT GRAIN

ALLAN CAMERON FRASER

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# THE INHERITANCE OF THE WEAK AWN IN CERTAIN AVENA CROSSES AND ITS RELATION TO OTHER CHARACTERS OF THE OAT GRAIN

# THE INHERITANCE OF THE WEAK AWN IN CERTAIN AVENA CROSSES AND ITS RELATION TO OTHER CHARACTERS OF THE OAT GRAIN[1]

ALLAN CAMERON FRASER

While several investigators have made studies of the inheritance of the strong awn in the genus Avena, relatively little attention has been given to the weak awn. Nilsson-Ehle (1914) was one of the first to discuss the weak awn, in his article on the inhibitor of awning. This writer was studying an awnless oat and a second variety which had an average of 54 per cent of awns. The facts concerning the inhibitor and its linkage with yellow were well established in the article, but no explanation was made as to the nature of the awning factor.

Love and Fraser (1917) published a preliminary report on the inheritance of the weak awn. This paper presents further data in support of the facts there stated, and goes further into the relationships of the awning factor and the conditions affecting it.

## MATERIALS USED

Three named varieties of oats were used in these studies — Burt, Sixty Day, and Early Ripe. The variety Early Ripe answers the descriptions of Burt in every detail and is apparently identical with it; therefore in reality only two varieties were used, Burt and Sixty Day.

The Burt oat as grown at this experiment station is dull red or yellowish red in color. The lower grain of the spikelet is usually awned, and frequently an awn is found on the upper grain as well. The awns are weak, seldom if ever twisted, and without a knee. Basal hairs are usually present at the sides of the basal callus only. These are fine, dense, and of medium length. The lower kernel has an articulation much like that of *Avena sterilis*.

The Sixty Day oat used was bright straw yellow in color. In no case were any awns found on either kernel of the spikelet, altho numerous

[1] Paper no. 74, Department of Plant Breeding, Cornell University, Ithaca, New York.

AUTHOR'S ACKNOWLEDGMENT. The writer wishes to make acknowledgment of the help given him by Professor H. H. Love, under whose direction these investigations were made and to express his appreciation of the valuable suggestions and criticisms offered by Professor Love.

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pure-line cultures were grown from the parent seed and there was ample opportunity for awns to appear had there been a tendency for the variety to produce them. Basal hairs were seldom present, and when found were very few, short, and scattered. The articulation was of the customary *A. sativa* type, with the erect and pinched-up opening.

These descriptions differ somewhat from the descriptions given by Etheridge (1916) for Burt and Sixty Day. In his publication the variety Burt is described as dull yellow in color and the Sixty Day as white. All the samples of Sixty Day which the writer has seen, however, have been yellow.

The plants of the Burt and Sixty Day varieties which were used in the crosses to be reported upon, came from pure-line cultures. These cultures were uniform within themselves. Successive pure-line cultures from the parents showed the characters described above.

These two varieties are concerned in the following pedigrees:

514 — Early Ripe (Burt) x Sixty Day
2501 b — Burt x Sixty Day
2501 ar — Sixty Day x Burt
2502 — Sixty Day x Burt

## METHODS OF STUDY

The parent plants and the first-generation hybrids were grown in the greenhouse. All crosses were made inside. The second and subsequent generations were grown in the field, and with these were grown a number of rows of the parent varieties in pure lines for the purpose of comparison.

In the case of the first-generation plants, in which the numbers were small, it was possible to study all the spikelets on each plant. With the much larger second and third generations, however, such a method would have been very wasteful of time, and therefore in these cases the study was limited to one representative panicle from each plant. The spikelets were picked from such a panicle, examined for awns, and placed in a small seed envelope, on which were recorded the data as to total number of spikelets on the panicle, number with one awn, and number with two awns.

It may be thought that the use of but one panicle from a plant would tend to give data which were incomplete and which perhaps did not

express the truth regarding that plant. However, as all panicles of the same plant have the same inheritance, the variation between them is of the nature of fluctuation and hence of no genetic significance. In practically every case the main culm was selected, since this was thought to be the most representative culm of the plant. In a study of the hulled and the hull-less condition, Love (Love and McRostie, 1919) has shown a close relation between the data on the main culm and those on the whole plant. An average of the panicles of a plant might possibly be a more nearly accurate measure of its value with respect to any character than would a single panicle. It must be remembered, however, that the whole plant may be a fluctuation from its own genotype. In such a case an average leads but little nearer the truth. In consideration of these facts it is felt that the use of one panicle from a plant is permissible, since it gives perhaps as nearly accurate a value of any character as can be had and gives it with a minimum of labor. Of the several characters studied, only one could be affected by the choice of panicle, and that is the proportion of awns.

## INHERITANCE OF THE WEAK AWN

### *Types of awns*

The awn of the oat is an extension of the midrib of the lemma, which rises from about the middle of the dorsal side of the grain. For convenience, awns are here classified under three headings — strong, intermediate, and weak. The strong awn is twisted at the base and is dark in color on the twisted part. At about one-third to three-eighths of the way up the awn there is a sharp bend, or knee, from which the awn proceeds almost at right angles to its former course. The strong awn is usually rather stiff and long. The intermediate awn lacks the geniculation of the strong awn and is less stiff. It is generally twisted at the base and dark in color on the twisted part, and it is often curved. The weak awn lacks the tendency to twist, the dark color, and the knee. It is usually straight or nearly so from the point of attachment, and is much less rigid than either the strong or the intermediate type. The weak awns may vary greatly in length, thickness, and rigidity. In some cases they are hair-like and very short, and are to be distinguished only by careful observation. As awns of this type become weaker, they are

produced nearer to the tip of the grain; that is, the midrib of the lemma adheres to the lemma for a greater distance before rising as an awn. In both the wild and the cultivated types of oats, the awns are either characteristically strong, weak, or lacking altogether. In hybrids of these, however, the awns may present all gradations between the awnless and the very strongly awned types. It is usually possible to classify these without any great difficulty as strong, intermediate, or weak (figs. 104 and 105).

### *$F_1$ of the cross Weak Awn × Awnless*

Several direct and reciprocal crosses between Burt and Sixty Day gave $F_1$ plants which were somewhat variable but which could be considered awnless. A few plants exhibited a very low proportion of awns, while most of the plants lacked awns altogether. The results of the $F_2$ generation, given in table 3 (page 641) and discussed later, show that these partly awned plants of $F_1$ are similar in genetic constitution to the awnless plants.

### *$F_2$ of the cross Weak Awn × Awnless*

The second generations of these crosses gave plants with all degrees of awning. Two types stood out distinctly — the fully awned and the awnless. Between these types the percentage of awns to the panicle varied from 1 to 99. The data for the second generation are given in table 1, arranged according to percentage of awns. For convenience a class range of 10 per cent is used, except in the case of the parent types, which are distinct enough to stand by themselves, and in the case of the 91–99 class, which had to be shortened to provide the 100-per-cent class. These minor inconsistencies could have no effect on the conclusions drawn from table 1.

The occurrence of a graded series between the parental types at first suggests a multiple-factor basis for awning. When the data are examined, however, it is apparent that the distribution does not satisfy such an hypothesis. The parental types occur with too great frequency. It is further evident from the data that no readjustment of class ranges will give a distribution which accords with a multiple-factor hypothesis.

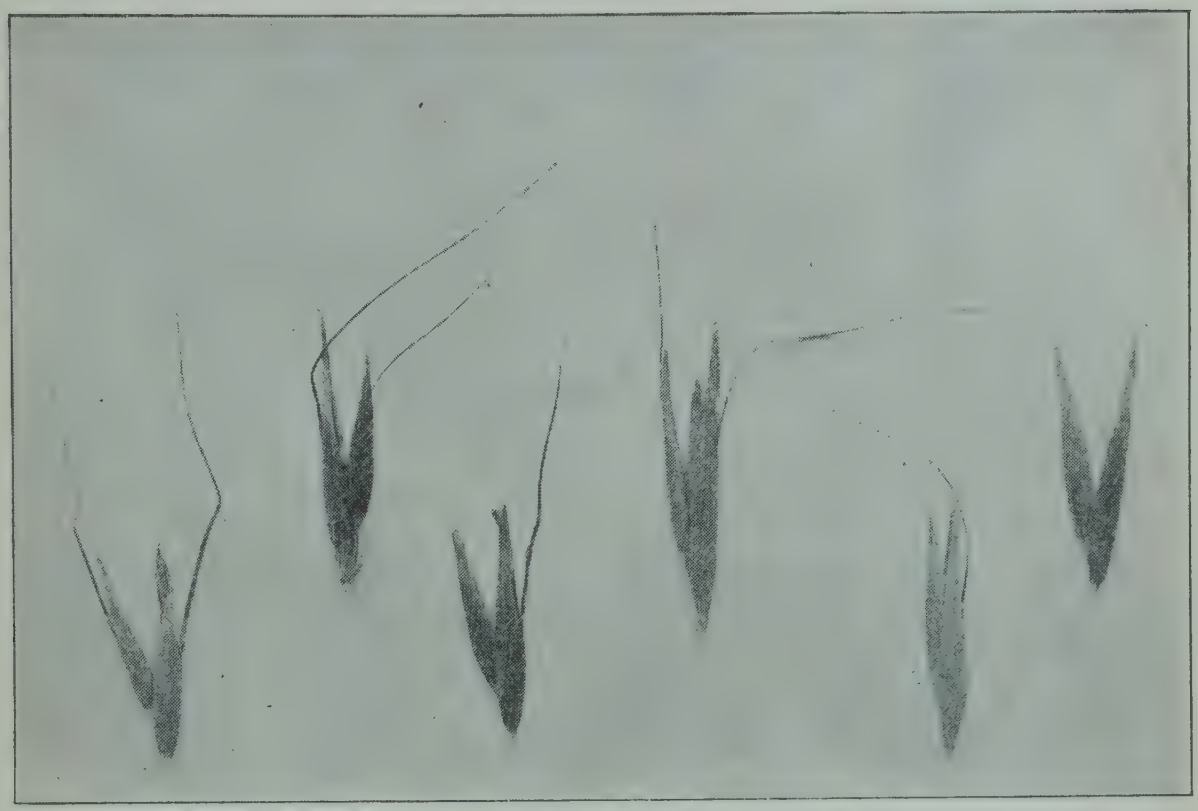

FIG. 104. GRADATIONS BETWEEN THE SPIKELET POSSESSING TWO STRONG AWNS, AND THE AWNLESS SPIKELET

From left to right are shown: two strong awns; one strong and one weak awn; one strong awn; two weak awns; one weak awn; and the awnless type

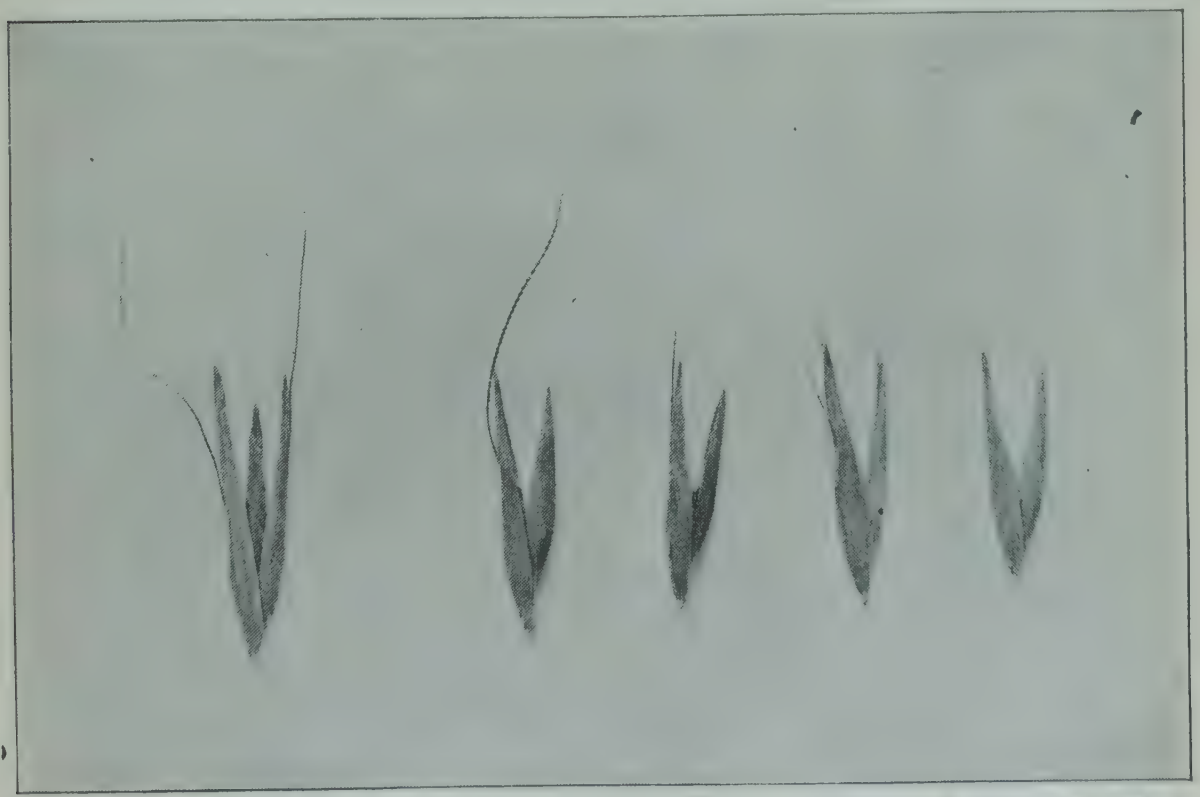

FIG. 105. GRADATIONS IN THE WEAK-AWN SERIES, FROM A SPIKELET HAVING TWO WEAK AWNS DOWN TO THE AWNLESS TYPE

TABLE 1. $F_2$ FREQUENCY DISTRIBUTION OF THREE FAMILIES WITH RESPECT TO PERCENTAGE OF AWNS

| Percentage of awns | Number of individuals | | | |
|---|---|---|---|---|
| | Pedigree 514 | Pedigree 2501 | Pedigree 2502 | Total |
| 0 | 110 | 48 | 14 | 172 |
| 1–10 | 29 | 34 | 14 | 77 |
| 11–20 | 23 | 30 | 5 | 58 |
| 21–30 | 25 | 24 | 1 | 50 |
| 31–40 | 18 | 20 | 4 | 42 |
| 41–50 | 18 | 32 | 4 | 54 |
| 51–60 | 14 | 16 | 6 | 36 |
| 61–70 | 8 | 16 | 6 | 30 |
| 71–80 | 12 | 7 | 6 | 25 |
| 81–90 | 5 | 15 | 7 | 27 |
| 91–99 | 12 | 6 | 1 | 19 |
| 100 | 66 | 92 | 22 | 180 |
| Total | 340 | 340 | 90 | 770 |

When all the partly-awned plants are grouped together and compared with the parental classes (table 2), the data agree fairly well with the expectancy based on a 1:2:1 ratio. The ratio of awnless:partly-awned: fully-awned is 172:418:180. The corresponding expectancies are 192.5:385:192.5.

TABLE 2. $F_2$ DISTRIBUTION OF THREE FAMILIES WITH RESPECT TO AWNS

| Pedigree | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Ratio per 4 | Deviation | Probable error | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|---|
| 514 | 110 | 164 | 66 | 274 | 66 | 3.22:0.78 | .22 | .06 | 3.67 |
| 2501 | 48 | 200 | 92 | 248 | 92 | 2.92:1.08 | .08 | .06 | 1.33 |
| 2502 | 14 | 54 | 22 | 68 | 22 | 3.02:0.98 | .02 | .12 | 0.17 |
| Observed total | 172 | 418 | 180 | 590 | 180 | 3.06:0.94 | .06 | .04 | 1.50 |
| Calculated total | 192.5 | 385.0 | 192.5 | 577.5 | 192.5 | | | | |

A comparison of the frequencies of plants not fully awned and those fully awned shows that the former occur about three times as often as the latter (table 2). Data presented subsequently show that the fully awned type is the pure recessive. On the assumption of a difference of

one factor between the fully awned and the awnless plants, a ratio of three plants not fully awned to one plant fully awned would be expected. The agreement between observed and calculated frequencies is close enough to bear out this assumption. A total of 770 plants gives a ratio of 590:180, or, on a basis of four, 3.06:0.94. The deviation from the expected ratio in this case is less than twice the probable error, and hence is not unduly large. While the deviation of pedigree 514 is 3.67 times as great as the probable error, such a deviation is not unreasonably large. The data clearly fit a 3:1 expectancy.

Additional data to prove this 3:1 relationship of plants not fully awned to those fully awned are presented in table 13. These are discussed later.

In order to ascertain whether or not there was any difference between the partly awned and the awnless plants of $F_1$, the progeny of such $F_1$ plants were kept separate. The results of such a test are shown in table 3. It is apparent from the results that the $F_1$ plants are alike, and that any appearances of segregation are misleading. Pedigree 2501 ar 2, a selection from awnless $F_1$ plants, has, if anything, a slightly higher percentage of fully awned plants in $F_2$ than have the offspring of the plants which showed a tendency to produce awns in $F_1$.

TABLE 3. $F_2$ DISTRIBUTION OF PEDIGREE 2501 WITH RESPECT TO AWNS

| Pedigree | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Ratio per 4 | Deviation | Probable error | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|---|
| 2501 b 1..... | 26 | 96 | 43 | 122 | 43 | 2.96:1.04 | .04 | .09 | 0.44 |
| 2501 ar 1..... | 17 | 61 | 28 | 78 | 28 | 2.94:1.06 | .06 | .11 | 0.55 |
| 2501 ar 2..... | 4 | 32 | 17 | 36 | 17 | 2.72:1.28 | .28 | .16 | 1.75 |
| 2501 ar 3..... | 1 | 11 | 4 | 12 | 4 | 3.00:1.00 | .00 | .29 | 0.00 |
| Total..... | 48 | 200 | 92 | 248 | 92 | 2.92:1.08 | .08 | .06 | 1.33 |

2501 b 1 = Burt × Sixty Day.
2501 ar 1 = Sixty Day × Burt — selection of partly awned $F_1$ plants.
2501 ar 2 = Sixty Day × Burt — selection of awnless $F_1$ plants.
2501 ar 3 = Sixty Day × Burt — unselected $F_1$ plants.

### *$F_3$ of the cross Weak Awn × Awnless*

A number of second-generation plants were tested in the third generation by individual plant-to-row cultures, with the following results:

*Behavior of the partly awned $F_2$ plants in $F_3$.*— From the fact that the partly awned plants in $F_2$ bear a 2:1 relation to each parent, one might

naturally assume that all such plants are heterozygous for the awning factor. With a few exceptions this is the case. When the $F_2$ plant is really partly awned, it behaves like an $F_1$ which is heterozygous for awning, and produces in the next generation three plants not fully awned to one fully awned.

The data on $F_3$ from twelve partly awned $F_2$ plants of pedigree 514 a 1 are given in table 4. In this case the ratio 1 awnless:2 partly awned:1

TABLE 4. BEHAVIOR OF PARTLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 514

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Percentage fully awned | Percentage of awns on partly awned plants |
| 514 a 1– 55 | 77 | 13 | 16 | 11 | 29 | 11 | 27.5 | 6.7 |
| –100 | 24 | 36 | 17 | 19 | 53 | 19 | 26.4 | 14.0 |
| –116 | 12 | 30 | 7 | 16 | 37 | 16 | 30.2 | 11.7 |
| –119 | 20 | 17 | 8 | 11 | 25 | 11 | 30.5 | 27.1 |
| –128 | 87 | 24 | 11 | 12 | 35 | 12 | 25.5 | 14.7 |
| –138 | 32 | 13 | 15 | 5 | 28 | 5 | 15.2 | 10.2 |
| –172 | 15 | 26 | 6 | 8 | 32 | 8 | 20.0 | 5.1 |
| –194 | 14 | 36 | 19 | 11 | 55 | 11 | 16.7 | 6.2 |
| –200 | 18 | 24 | 12 | 11 | 36 | 11 | 23.4 | 11.3 |
| –216 | 30 | 11 | 18 | 8 | 29 | 8 | 21.6 | 12.1 |
| –244 | 60 | 13 | 17 | 7 | 30 | 7 | 18.9 | 25.1 |
| –264 | 81 | 23 | 6 | 10 | 29 | 10 | 25.6 | 23.0 |
| Total | | 266 | 152 | 129 | 418 | 129 | 23.6 | |

fully awned, is not preserved. The ratio of plants not fully awned to those fully awned, however, is a good 3:1 ratio. The totals 418 and 129 are in the ratio of 3.06:0.94. The deviation in this case is 0.06 and the probable error is $\pm 0.05$. The deviation, then, is only 1.2 times as large as the probable error, and is therefore well within the limits of reason. From the column giving the percentage of fully awned plants, it can be seen that, while there is more or less variation among the different cultures, there is a tendency to produce about 25 per cent of fully awned plants in each one.

The last two columns of tables 4, 5, and 6 are used later in tracing the relation between the percentage of awns on the $F_2$ parent and certain characteristics in its offspring.

In table 5 are given the data on forty-nine pedigrees which were partly awned in $F_2$ and which show in $F_3$ a 3:1 ratio of plants not fully awned to plants fully awned. While there is a somewhat wide variation in per-

TABLE 5. BEHAVIOR OF PARTLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 2501

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Percentage fully awned | Percentage of awns on partly awned plants |
| 2501 b 1 – 3 | 35 | 9 | 7 | 9 | 16 | 9 | 36.0 | 21.0 |
| – 8 | 22 | 4 | 11 | 2 | 15 | 2 | 11.8 | 30.0 |
| – 10 | 11 | 3 | 14 | 9 | 17 | 9 | 34.6 | 20.0 |
| – 16 | 7 | 4 | 17 | 8 | 21 | 8 | 27.6 | 43.0 |
| – 22 | 11 | 5 | 3 | 2 | 8 | 2 | 20.0 | 37.0 |
| – 24 | 71 | 1 | 6 | 10 | 7 | 10 | 58.8 | 56.0 |
| – 28 | 9 | 1 | 11 | 6 | 12 | 6 | 33.3 | 22.8 |
| – 31 | 15 | 9 | 13 | 2 | 22 | 2 | 8.3 | 10.0 |
| – 35 | 59 | 3 | 9 | 7 | 12 | 7 | 36.8 | 44.0 |
| – 45 | 43 | 4 | 16 | 4 | 20 | 4 | 16.7 | 59.0 |
| – 52 | 60 | 0 | 5 | 2 | 5 | 2 | 28.6 | 64.0 |
| – 53 | 35 | 6 | 13 | 6 | 19 | 6 | 24.0 | 35.0 |
| – 59 | 24 | 5 | 10 | 2 | 15 | 2 | 11.8 | 17.7 |
| – 60 | 50 | 4 | 9 | 4 | 13 | 4 | 23.5 | 30.0 |
| – 62 | 65 | 2 | 11 | 5 | 13 | 5 | 27.8 | 45.2 |
| – 66 | 71 | 5 | 11 | 5 | 16 | 5 | 23.8 | 44.0 |
| – 67 | 30 | 4 | 14 | 5 | 18 | 5 | 21.7 | 37.8 |
| – 72 | 4 | 7 | 17 | 9 | 24 | 9 | 27.3 | 19.1 |
| – 74 | 63 | 1 | 15 | 5 | 16 | 5 | 23.8 | 46.1 |
| – 76 | 39 | 2 | 9 | 10 | 11 | 10 | 47.6 | 32.2 |
| – 78 | 31 | 1 | 11 | 7 | 12 | 7 | 36.8 | 48.0 |
| – 81 | 86 | 4 | 9 | 2 | 13 | 2 | 13.3 | 51.5 |
| – 87 | 13 | 3 | 8 | 6 | 11 | 6 | 35.3 | 40.0 |
| – 89 | 27 | 1 | 10 | 7 | 11 | 7 | 38.9 | 34.7 |
| –100 | 96 | 4 | 16 | 7 | 20 | 7 | 25.9 | 42.1 |
| –101 | 12 | 8 | 13 | 7 | 21 | 7 | 25.0 | 13.7 |
| –103 | 61 | 3 | 18 | 4 | 21 | 4 | 16.0 | 35.6 |
| –104 | 12 | 6 | 15 | 1 | 21 | 1 | 4.5 | 21.1 |
| –105 | 58 | 3 | 6 | 3 | 9 | 3 | 25.0 | 44.1 |
| –106 | 45 | 10 | 12 | 5 | 22 | 5 | 18.5 | 45.0 |
| –110 | 8 | 2 | 9 | 4 | 11 | 4 | 26.7 | 30.5 |
| –112 | 65 | 1 | 20 | 5 | 21 | 5 | 19.2 | 40.0 |
| –119 | 46 | 0 | 13 | 8 | 13 | 8 | 38.1 | 37.6 |
| –121 | 83 | 4 | 4 | 3 | 8 | 3 | 27.3 | 8.4 |
| –126 | 64 | 3 | 9 | 5 | 12 | 5 | 29.4 | 27.2 |
| –127 | 15 | 8 | 13 | 1 | 21 | 1 | 4.5 | 13.7 |
| –128 | 31 | 5 | 17 | 4 | 22 | 4 | 15.4 | 27.8 |
| –134 | 62 | 2 | 10 | 6 | 12 | 6 | 33.3 | 40.4 |
| –141 | 7 | 15 | 5 | 3 | 20 | 3 | 13.0 | 30.0 |
| –142 | 60 | 3 | 3 | 4 | 6 | 4 | 40.0 | 14.0 |
| –145 | 83 | 0 | 8 | 6 | 8 | 6 | 42.8 | 61.4 |
| –151 | 15 | 5 | 5 | 8 | 10 | 8 | 44.4 | 8.2 |
| –159 | 41 | 0 | 10 | 5 | 10 | 5 | 33.3 | 35.6 |
| –164 | 8 | 5 | 9 | 1 | 14 | 1 | 6.7 | 8.0 |
| 2501 ar 1– 15 | 89 | 2 | 11 | 10 | 13 | 10 | 43.5 | 38.0 |
| – 18 | 24 | 6 | 12 | 3 | 18 | 3 | 14.3 | 18.0 |
| – 42 | 72 | 1 | 15 | 6 | 16 | 6 | 27.3 | 33.0 |
| – 53 | 22 | 7 | 19 | 6 | 26 | 6 | 18.8 | 33.0 |
| 2501 ar 2– 11 | 91 | 1 | 6 | 4 | 7 | 4 | 36.4 | 40.6 |
| Total | ..... | 192 | 537 | 253 | 729 | 253 | 25.8 | ..... |

centage of fully awned plants in the different cultures, the total of all shows that these deviations tend to offset one another. Such deviations are to be expected within individual cultures when the numbers are comparatively small.

Of a total of 982 third-generation plants from pedigree 2501, 729 were not fully awned and 253 were fully awned. The ratio, on the basis of four, is 2.97:1.03, and the deviation from the expected ratio is 0.03. This deviation is equal to the probable error for this number of plants.

The data in table 5, therefore, give a ratio which is in close agreement with the 3:1 ratio expected. The slight deviation from this ratio is well within reason. Clearly the $F_2$ plants tested here are heterozygous for the awning factor.

A number of irregular cases from family 2501 are presented in tables 5 A and 5 B. These pedigrees seemed not properly to belong in table 5, and to include them in that table would render the total figures subject to question.

In table 5 A are included those cultures which, tho producing a small percentage of awns in $F_2$, were potentially awnless. It is seen from the

TABLE 5 A. IRREGULAR CASES FROM SERIES 2501

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Percentage of awnless in $F_3$ | Number of awned spikelets | Total number of spikelets | Percentage of awns in series |
| 2501 b 1 – 15..... | 4 | 20 | 2 | 0 | 90.9 | 2 | 323 | 0.6 |
| – 19..... | 7 | 25 | 1 | 0 | 96.2 | 1 | 486 | 0.2 |
| – 39..... | 12 | 14 | 10 | 0 | 58.3 | 18 | 380 | 4.7 |
| – 47..... | 18 | 16 | 13 | 0 | 55.2 | 64 | 837 | 7.6 |
| – 54..... | 14 | 15 | 2 | 0 | 88.2 | 9 | 391 | 2.3 |
| –138..... | 11 | 9 | 4 | 0 | 69.2 | 4 | 152 | 2.6 |
| –147..... | 4 | 15 | 11 | 0 | 57.7 | 34 | 587 | 5.8 |
| 2501 ar 1– 27..... | 18 | 8 | 12 | 0 | 40.0 | 19 | 135 | 6.0 |
| – 55..... | 6 | 4 | 4 | 0 | 50.0 | 6 | 181 | 3.3 |
| Total..... | ..... | 126 | 59 | 0 | 68.1 | 157 | 3,652 | 4.3 |

last column of the table that none of these pedigrees produced over 7.6 per cent of awns on all the third-generation plants. A comparison of the number of awned spikelets with the total number of spikelets in each series shows how slight was the tendency to produce awns. Five of the $F_2$ parents had only one awn, while one had two, one had three, and two had five. In the light of these facts it seems reasonable to assume that these pedigrees are potentially awnless, but are for some reason producing a few awns.

In table 5 B are included those pedigrees in which there was a change, on the part of some of the awns at least, to intermediate and strong awns.

TABLE 5 B. IRREGULAR CASES FROM SERIES 2501

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | |
|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Number of strong awns | Number of intermediate awns |
| 2501 b 1– 40..... | 6 | 15 | 10 | 1 | 0 | 4 |
| – 64..... | 25 | 13 | 5 | 0 | 3 | 0 |
| – 73..... | 24 | 2 | 15 | 1 | 10 | 2 |
| –108..... | 69 | 2 | 8 | 1 | 2 | 2 |
| –117..... | 50 | 2 | 20 | 0 | 10 | 10 |
| –139..... | 16 | 0 | 17 | 0 | 0 | 24 |
| –158..... | 3 | 4 | 25 | 0 | 14 | 21 |
| Total..... | ..... | 38 | 100 | 3 | 39 | 63 |

Such a change has occurred in a number of the pedigrees studied, and in nearly every case it has brought about irregularities in the production of awns. It seems quite probable that a change in the awns so radical as to make strong and intermediate awns from weak ones might have an effect on the factor for awning.

The fact that there is shown in this table no regularity in the appearance of awnless, partly awned, and fully awned $F_3$ plants, may possibly be ascribed to the influence of environment. Pure-line studies[2] with the variety Burt and with the species *Avena fatua* have shown that in the case of these fully awned types environment has little influence on the number of awns produced. In the variety Black Mesdag, however, in which the percentage of awns is not uniform and is less than 100, environment seems to have a strong influence on the number of awns produced.

Data on the $F_2$ of a third family, 2502, are given in table 6. Here again more or less variation is to be noted among the separate cultures, with a general tendency to produce about 25 per cent of fully awned plants.

The totals in table 6 do not present as good a 3:1 ratio as do those in table 5. The tendency toward such a ratio, however, is fairly strong. The ratio per four is 2.81:1.19, with a probable error of $\pm 0.04$. A com-

[2] Unpublished data of studies by H. H. Love.

TABLE 6. BEHAVIOR OF PARTLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 2502

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Percentage fully awned | Percentage of awns on partly awned plants |
| 2502 a 1– 2 | 7 | 7 | 12 | 7 | 19 | 7 | 26.9 | 22.7 |
| – 3 | 3 | 2 | 9 | 6 | 11 | 6 | 35.3 | 26.9 |
| – 4 | 86 | 3 | 11 | 7 | 14 | 7 | 33.3 | 59.2 |
| – 5 | 65 | 1 | 18 | 7 | 19 | 7 | 26.9 | 49.0 |
| – 7 | 24 | 5 | 13 | 6 | 18 | 6 | 25.0 | 27.9 |
| – 9 | 75 | 1 | 12 | 7 | 13 | 7 | 35.0 | 48.4 |
| –12 | 75 | 2 | 9 | 2 | 11 | 2 | 15.4 | 38.2 |
| –16 | 70 | 0 | 8 | 10 | 8 | 10 | 55.6 | 62.5 |
| –17 | 80 | 2 | 12 | 10 | 14 | 10 | 41.7 | 63.8 |
| –19 | 63 | 3 | 11 | 8 | 14 | 8 | 36.4 | 47.3 |
| –20 | 76 | 0 | 15 | 8 | 15 | 8 | 34.8 | 61.5 |
| –23 | 51 | 0 | 15 | 6 | 15 | 6 | 28.6 | 46.7 |
| –24 | 4 | 11 | 4 | 5 | 15 | 5 | 25.0 | 27.8 |
| –32 | 16 | 3 | 10 | 9 | 13 | 9 | 40.9 | 36.0 |
| –35 | 17 | 4 | 11 | 8 | 15 | 8 | 34.8 | 39.0 |
| –36 | 13 | 1 | 3 | 5 | 4 | 5 | 55.6 | 8.2 |
| –37 | 66 | 2 | 9 | 5 | 11 | 5 | 31.2 | 38.6 |
| –38 | 66 | 1 | 10 | 4 | 11 | 4 | 26.7 | 48.2 |
| –41 | 83 | 0 | 10 | 7 | 10 | 7 | 41.2 | 77.2 |
| –42 | 67 | 0 | 4 | 12 | 4 | 12 | 75.0 | 76.7 |
| –43 | 81 | 1 | 11 | 9 | 12 | 9 | 42.9 | 37.0 |
| –46 | 83 | 0 | 10 | 4 | 10 | 4 | 28.6 | 70.0 |
| –47 | 5 | 3 | 10 | 1 | 13 | 1 | 7.1 | 35.3 |
| –49 | 83 | 1 | 9 | 11 | 10 | 11 | 52.4 | 50.5 |
| –52 | 4 | 7 | 17 | 3 | 24 | 3 | 11.1 | 45.8 |
| –55 | 19 | 7 | 11 | 5 | 18 | 5 | 21.7 | 38.5 |
| –57 | 45 | 2 | 21 | 5 | 23 | 5 | 17.9 | 64.1 |
| –60 | 94 | 1 | 14 | 6 | 15 | 6 | 28.6 | 57.5 |
| –64 | 43 | 5 | 13 | 4 | 18 | 4 | 18.2 | 32.5 |
| –66 | 88 | 0 | 11 | 9 | 11 | 9 | 45.0 | 75.0 |
| –68 | 84 | 0 | 10 | 7 | 10 | 7 | 41.2 | 70.8 |
| –69 | 75 | 3 | 10 | 0 | 13 | 0 | 0.0 | 25.6 |
| –71 | 57 | 2 | 10 | 3 | 12 | 3 | 20.0 | 47.0 |
| –75 | 58 | 0 | 6 | 6 | 6 | 6 | 50.0 | 57.4 |
| –78 | 52 | 2 | 13 | 2 | 15 | 2 | 11.8 | 60.0 |
| –82 | 70 | 2 | 6 | 2 | 8 | 2 | 20.0 | 43.2 |
| –84 | 50 | 3 | 22 | 5 | 25 | 5 | 16.7 | 40.3 |
| –85 | 10 | 12 | 14 | 0 | 26 | 0 | 0.0 | 23.8 |
| –86 | 31 | 2 | 10 | 6 | 12 | 6 | 33.3 | 60.1 |
| –89 | 57 | 3 | 5 | 3 | 8 | 3 | 27.3 | 26.2 |
| Total | ..... | 104 | 439 | 230 | 543 | 230 | 29.8 | ..... |

parison of the deviation, 0.19, with the probable error, shows the former to be 4.75 times as great as the latter.

Family 2502 a 1, like family 2501, presents certain irregular cases in $F_3$. These are grouped in table 6 A. Pedigrees 2502 a 1–6 and 2502 a 1–13 appear to be similar to those in table 5 A; that is, they are potentially awnless. The former pedigree has only 6 awns on 541 spikelets, or 1.11 per cent of awns, in $F_3$; its parent had only 1 awn on 18 spikelets. Pedigree 2502 a 1–13 has only 1.97 per cent of awns in $F_3$; its parent had 2 awns on 23 spikelets.

TABLE 6 A. IRREGULAR CASES FROM SERIES 2502

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned | Number of strong awns | Number of intermediate awns | Number of awned spikelets | Total number of spikelets | Percentage of awns in series |
| 2502 a 1– 6 | 6 | 18 | 5 | 0 | 0 | 0 | 6 | 541 | 1.11 |
| –13 | 9 | 14 | 7 | 0 | 0 | 0 | 12 | 610 | 1.97 |
| Total | ..... | 32 | 12 | 0 | 0 | 0 | 18 | 1,151 | 1.56 |
| 2502 a 1– 1 | 33 | 2 | 21 | 0 | 15 | 15 | ..... | ..... | ..... |
| –30 | 18 | 0 | 21 | 0 | 2 | 35 | ..... | ..... | ..... |
| –33 | 3 | 8 | 21 | 0 | 3 | 20 | ..... | ..... | ..... |
| –34 | 5 | 1 | 16 | 0 | 0 | 6 | ..... | ..... | ..... |
| –44 | 6 | 0 | 18 | 0 | 24 | 43 | ..... | ..... | ..... |
| –56 | 8 | 5 | 18 | 0 | 11 | 36 | ..... | ..... | ..... |
| –59 | 4 | 7 | 19 | 0 | 43 | 40 | ..... | ..... | ..... |
| –61 | 10 | 1 | 17 | 0 | 18 | 27 | ..... | ..... | ..... |
| –62 | 50 | 2 | 13 | 0 | 0 | 6 | ..... | ..... | ..... |
| –63 | 5 | 6 | 16 | 0 | 1 | 11 | ..... | ..... | ..... |
| –83 | 37 | 2 | 22 | 0 | 8 | 18 | ..... | ..... | ..... |
| Total | ..... | 34 | 202 | 0 | 125 | 257 | ..... | ..... | ..... |

The remainder of the cultures recorded in table 6 A are like those in table 5 B. In these the factor for awning has been upset by the production of intermediate and strong awns.

It is apparent from these data that nearly all the partly awned $F_2$ plants are heterozygotes. Some of the plants which have a very low percentage of awns evidently belong with the awnless plants of $F_2$. Others with an equally low percentage of awns are true heterozygotes and seem to produce as high a percentage of fully awned plants in $F_2$ as do plants having 90 per cent of awns. Only by the breeding test can distinction be made between the two classes of plants having a very low percentage of awns in $F_2$.

*Behavior of the awnless $F_2$ plants in $F_3$.*—A number of awnless $F_2$ plants were selected from each family for a test in $F_3$. Their behavior is recorded in tables 7, 8, and 9.

In family 514 a 1 (table 7), eleven such awnless pedigrees were studied. Five of these bred true to the awnless condition, giving a total of 249 plants. The remaining six segregated to give approximately the ratio of 3 plants not fully awned to 1 fully awned in each case. The totals of these six pedigrees are in the ratio of 2.97 to 1.03, with the deviation less than half the probable error.

TABLE 7. BEHAVIOR OF AWNLESS $F_2$ PLANTS IN $F_3$. SERIES 514

| Pedigree | $F_3$ progeny | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Ratio per 4 | Deviation | Probable error | Dev. / P. E. |
| 514 a 1– 34 | 48 | 0 | 0 | 48 | 0 | ..... | ..... | ..... | ..... |
| –126 | 75 | 0 | 0 | 75 | 0 | ..... | ..... | ..... | ..... |
| –185 | 31 | 0 | 0 | 31 | 0 | ..... | ..... | ..... | ..... |
| –232 | 63 | 0 | 0 | 63 | 0 | ..... | ..... | ..... | ..... |
| –336 | 32 | 0 | 0 | 32 | 0 | ..... | ..... | ..... | ..... |
| Total | 249 | 0 | 0 | 249 | 0 | ..... | ..... | ..... | ..... |
| 514 a 1– 36 | 52 | 3 | 15 | 55 | 15 | 3.14:0.86 | .14 | .14 | 1.00 |
| –176 | 26 | 6 | 11 | 32 | 11 | 2.98:1.02 | .02 | .18 | 0.11 |
| –221 | 11 | 4 | 7 | 15 | 7 | 2.73:1.27 | .27 | .25 | 1.08 |
| –247 | 18 | 7 | 15 | 25 | 15 | 2.50:1.50 | .50 | .18 | 2.78 |
| –291 | 29 | 3 | 11 | 32 | 11 | 2.98:1.02 | .02 | .18 | 0.11 |
| –339 | 34 | 0 | 8 | 34 | 8 | 3.24:0.76 | .24 | .18 | 1.33 |
| Total | 170 | 23 | 67 | 193 | 67 | 2.97:1.03 | .03 | .07 | 0.43 |

Twenty-eight pedigrees of awnless plants from family 2501 were tested in $F_3$. Data on these are given in table 8. Eighteen pedigrees bred practically true for awnlessness. Only one of these produced entirely awnless plants; the others produced in each case a few partly awned plants. In practically every case, however, the percentage of awns was very low, being higher than 2 per cent in only a few instances. Just why these plants, which might have been expected to produce only awnless plants, should have produced a small percentage of awns, it is difficult to say. The environmental conditions of 1917 were unusual, and they may have had some part in producing these awns. If the factor for the awnless condition is considered as a definite allelomorph of the factor for the fully awned condition, as *A* and *a*, then it is hard to explain why plants of the supposed constitution *AA* should produce any awns whatever. If, on the other hand, it is assumed that both parents carry the factor for awning, and that this factor is suppressed in the variety Sixty Day by an inhibitor, it is possible to explain certain of these irregularities in the inheritance of awns. In the case at hand it might be assumed that the inhibitory factors did not function to completely prevent the production of awns. It seems quite probable that the latter assumption is correct. At least it has been proved (Love and Craig, 1918) that the variety Sixty Day carries a factor inhibitory to awning and that this factor is closely linked with the factor for yellow color.

TABLE 8. BEHAVIOR OF AWNLESS $F_2$ PLANTS IN $F_3$. SERIES 2501

| Pedigree | $F_3$ progeny | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Number of awned spikelets | Total number of spikelets | Percentage of awns in series |
| 2501 b 1 – 6 | 15 | 3 | 0 | 18 | 0 | 5 | 431 | 1.2 |
| – 12 | 21 | 2 | 0 | 23 | 0 | 3 | 320 | 0.9 |
| – 17 | 17 | 4 | 0 | 21 | 0 | 13 | 593 | 2.2 |
| – 20 | 8 | 2 | 0 | 10 | 0 | 3 | 252 | 1.2 |
| – 21 | 17 | 2 | 0 | 19 | 0 | 2 | 691 | 0.3 |
| – 36 | 18 | 5 | 0 | 23 | 0 | 8 | 600 | 1.3 |
| – 37 | 23 | 0 | 0 | 23 | 0 | 0 | ..... | 0.0 |
| – 44 | 11 | 13 | 0 | 24 | 0 | 57 | 782 | *7.3 |
| – 56 | 6 | 2 | 0 | 8 | 0 | 8 | 143 | 5.6 |
| – 69 | 17 | 1 | 0 | 18 | 0 | 1 | 285 | 0.3 |
| – 71 | 17 | 7 | 0 | 24 | 0 | 14 | 732 | 1.9 |
| – 79 | 22 | 4 | 0 | 26 | 0 | 9 | 836 | 1.1 |
| – 99 | 15 | 11 | 0 | 26 | 0 | 17 | 858 | 2.0 |
| –122 | 21 | 8 | 0 | 29 | 0 | 13 | 940 | 1.4 |
| –137 | 8 | 2 | 0 | 10 | 0 | 4 | 188 | 2.1 |
| 2501 ar 1– 8 | 22 | 3 | 0 | 25 | 0 | 5 | 729 | 0.7 |
| – 39 | 16 | 1 | 0 | 17 | 0 | 24 | 434 | †5.5 |
| – 67 | 22 | 4 | 0 | 26 | 0 | 5 | 727 | 0.7 |
| Total | 293 | 74 | 0 | 370 | 0 | 191 | 9,541 | 2.00 |
| 2501 b 1 – 26 | 12 | 5 | 1 | 17 | 1 | ..... | ..... | ..... |
| – 65 | 3 | 6 | 6 | 9 | 6 | ..... | ..... | ..... |
| – 93 | 13 | 5 | 5 | 18 | 5 | ..... | ..... | ..... |
| –102 | 5 | 13 | 6 | 18 | 6 | ..... | ..... | ..... |
| 2501 ar 1– 10 | 19 | 3 | 5 | 22 | 5 | ..... | ..... | ..... |
| – 74 | 5 | 6 | 4 | 11 | 4 | ..... | ..... | ..... |
| – 94 | 9 | 3 | 2 | 12 | 2 | ..... | ..... | ..... |
| –105 | 8 | 1 | 1 | 9 | 1 | ..... | ..... | ..... |
| 2501 ar 2– 14 | 6 | 6 | 2 | 12 | 2 | ..... | ..... | ..... |
| 2501 ar 3– 15 | 10 | 8 | 4 | 18 | 4 | ..... | ..... | ..... |
| Total | 90 | 56 | 36 | 146 | 36 | ..... | ..... | ..... |

* One strong and two intermediate awns.
† All awns on one panicle.

The second part of table 8 shows a behavior similar to that recorded in table 7. The awnless plants of the second generation may be heterozygotes. Ten pedigrees from family 2501 gave a total of 146 plants not fully awned to 36 plants fully awned. The ratio per four for these data is 3.21:0.79. In this case the deviation, 0.21, is rather large; but the probable error, $\pm 0.09$, is also large, so that the deviation is only slightly over twice (2.33 times) as large as the probable error.

Data on the $F_3$ progeny of fourteen awnless $F_2$ plants of family 2502 are given in table 9. Three of these pedigrees were entirely awnless; five were practically awnless, having less than 5 per cent of awns; two had a rather high percentage of awns, pedigrees 2502 a 1–14 and 2502 a 1–

TABLE 9. BEHAVIOR OF AWNLESS $F_2$ PLANTS IN $F_3$. SERIES 2502

| Pedigree | $F_3$ progeny | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Number of awned spikelets | Total number of spikelets | Percentage of awns in series |
| 2502 a 1–10 | 25 | 0 | 0 | 25 | 0 | 0 | ..... | 0.0 |
| –14 | 5 | 14 | 0 | 19 | 0 | 115 | 634 | *18.1 |
| –22 | 11 | 12 | 0 | 23 | 0 | 24 | 748 | 3.2 |
| –31 | 16 | 5 | 0 | 21 | 0 | 18 | 471 | 3.8 |
| –39 | 16 | 0 | 0 | 16 | 0 | 0 | ..... | 0.0 |
| –45 | 18 | 0 | 0 | 18 | 0 | 0 | ..... | 0.0 |
| –72 | 3 | 5 | 0 | 8 | 0 | 23 | 301 | †7.6 |
| –76 | 13 | 4 | 0 | 17 | 0 | 8 | 567 | 1.4 |
| –77 | 6 | 11 | 0 | 17 | 0 | 39 | 744 | ‡5.2 |
| –79 | 8 | 2 | 0 | 10 | 0 | 4 | 228 | 1.8 |
| –81 | 4 | 11 | 0 | 15 | 0 | 53 | 389 | ‡13.6 |
| –87 | 13 | 12 | 0 | 25 | 0 | 40 | 852 | 4.7 |
| Total | 138 | 76 | 0 | 214 | 0 | 324 | 4,934 | 6.6 |
| 2502 a 1–54 | 7 | 13 | 1 | 20 | 1 | ..... | ..... | ..... |
| –67 | 7 | 17 | 1 | 24 | 1 | ..... | ..... | ..... |
| Total | 14 | 30 | 2 | 44 | 2 | ..... | ..... | ..... |

* Three strong awns and twenty-two intermediate awns.
† Five intermediate awns.
‡ Apparently segregating. Some spikelets over 50 per cent awned.

81, and from the data it seems likely that they were segregating for awns. Since no fully awned plants were produced, however, they were not entered with those plants which were segregating. Two other pedigrees with a high percentage of awns in $F_3$ were withheld from the main part of the table because of the appearance of strong and intermediate awns on a number of the grains. These two pedigrees, 54 and 67, each gave one fully awned plant. The data on these are averaged in with other data on heterozygous $F_2$ plants in table 13 (page 654).

*Behavior of the fully awned $F_2$ plants in $F_3$.*—Sixty fully awned plants of $F_2$ were tested in $F_3$. The results are given in tables 10, 11, and 12.

Three of the plants, in family 514 a 1, gave only fully awned plants, 103 in all (table 10).

In family 2501 (table 11), twenty-five pedigrees gave only fully awned plants, 465 in number. Pedigrees 2501 b 1–11, 2501 ar 1–71, and 2501 ar 1–75, apparently belong with the pedigrees in the first part of the table. For some reason these three series failed to produce only fully awned plants, but produced a very few partly awned plants. Possibly the rather unusual seasonal and environmental conditions of 1917 may account for this.

TABLE 10. BEHAVIOR OF FULLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 514

| Pedigree | Percentage of awns in $F_2$ | $F_3$ progeny | | |
|---|---|---|---|---|
| | | Awnless | Partly awned | Fully awned |
| 514 a 1–22 | 100 | 0 | 0 | 47 |
| –88 | 100 | 0 | 0 | 36 |
| –95 | 100 | 0 | 0 | 20 |
| Total | ..... | 0 | 0 | 103 |

Pedigrees 2501 b 1–49, 2501 ar 1–4, and 2501 ar 2–5 are irregular in producing a large number of partly awned plants. The parent of the first named had nine strong and two intermediate awns, however, and the series itself produced in $F_3$ eleven strong and fifty-three intermediate awns, while pedigree 2501 ar 2–5 produced ten strong and thirty-four intermediate awns in $F_3$. As has already been pointed out, the behavior of any pedigree is likely to be irregular when the plants produce strong and intermediate awns.

The last four pedigrees in the table have evidently segregated after the fashion of partly awned $F_2$ plants. The last column shows that in the case of three of these pedigrees there was only a small number of spikelets on the parent plant from which to judge as to whether it should be classed as partly awned or fully awned. Perhaps all these plants would have proved to be partly awned had there been a larger number of spikelets on which to base the classification.

Family 2502 a 1 (table 12) exhibits about the same behavior as does family 2501. Seventeen pedigrees produced only fully awned plants, 237 in all. Five pedigrees segregated in a manner which suggests a 3:1 ratio. The parent plants in each of these cases produced only a small number of spikelets. It is evident that these plants were wrongly classified in $F_2$.

A survey of tables 10, 11, and 12 shows that in every case in which the $F_2$ parent was actually a fully awned plant and in which no unusual phenomena occurred to upset the normal behavior of these plants, the plants having 100 per cent of awns in $F_2$ gave only fully awned plants in $F_3$. From this it is apparent that the fully awned condition is the pure recessive.

TABLE 11. BEHAVIOR OF FULLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 2501

| Pedigree | $F_3$ progeny | | | | Number of spikelets on $F_2$ parent |
|---|---|---|---|---|---|
| | Awnless | Partly awned | Fully awned | Percentage fully awned | |
| 2501 b 1 – 1 | 0 | 0 | 15 | 100 | 42 |
| – 4 | 0 | 0 | 26 | 100 | 23 |
| – 7 | 0 | 0 | 25 | 100 | 27 |
| – 25 | 0 | 0 | 12 | 100 | 26 |
| – 30 | 0 | 0 | 20 | 100 | 24 |
| – 32 | 0 | 0 | 20 | 100 | 23 |
| – 41 | 0 | 0 | 5 | 100 | 7 |
| – 43 | 0 | 0 | 19 | 100 | 16 |
| – 48 | 0 | 0 | 17 | 100 | 25 |
| – 50 | 0 | 0 | 21 | 100 | 14 |
| – 57 | 0 | 0 | 6 | 100 | 10 |
| – 77 | 0 | 0 | 24 | 100 | 12 |
| – 83 | 0 | 0 | 17 | 100 | 21 |
| – 86 | 0 | 0 | 29 | 100 | 23 |
| – 92 | 0 | 0 | 7 | 100 | 7 |
| – 96 | 0 | 0 | 20 | 100 | 25 |
| – 97 | 0 | 0 | 22 | 100 | 22 |
| –133 | 0 | 0 | 17 | 100 | 29 |
| 2501 ar 1– 30 | 0 | 0 | 24 | 100 | 33 |
| – 38 | 0 | 0 | 20 | 100 | 22 |
| – 59 | 0 | 0 | 24 | 100 | 21 |
| – 65 | 0 | 0 | 22 | 100 | 20 |
| – 85 | 0 | 0 | 23 | 100 | 15 |
| – 90 | 0 | 0 | 20 | 100 | 22 |
| 2501 ar 3– 4 | 0 | 0 | 10 | 100 | 19 |
| Total breeding true | ..... | ..... | 465 | ..... | ..... |
| 2501 b 1 – 11 | 0 | 1 | 25 | 96.1 | 27 |
| – 49 | 0 | 18 | 3 | 14.3 | *20 |
| 2501 ar 1– 4 | 0 | 15 | 8 | 34.8 | 21 |
| – 71 | 1 | 0 | 24 | 96.0 | 34 |
| – 75 | 0 | 1 | 13 | 92.9 | 12 |
| 2501 ar 2– 5 | 0 | 7 | 9 | 56.3 | †13 |
| Total | 1 | 42 | 82 | 65.6 | ..... |
| 2501 b 1 – 70 | 1 | 11 | 5 | 29.4 | 11 |
| – 75 | 2 | 11 | 6 | 31.6 | 12 |
| –120 | 1 | 11 | 12 | 50.0 | 19 |
| –155 | 4 | 12 | 6 | 27.3 | 44 |
| Total | 8 | 45 | 29 | 35.4 | ..... |

* Nine strong and two intermediate awns in parent; eleven strong and fifty-three intermediate in $F_3$.
† Ten strong and thirty-four intermediate awns in this series.

TABLE 12. BEHAVIOR OF FULLY AWNED $F_2$ PLANTS IN $F_3$. SERIES 2502

| Pedigree | $F_3$ progeny | | | | Number of spikelets on $F_2$ parent |
|---|---|---|---|---|---|
| | Awnless | Partly awned | Fully awned | Percentage fully awned | |
| 2502 a 1– 8 | 0 | 0 | 20 | 100 | 23 |
| –11 | 0 | 0 | 19 | 100 | 24 |
| –15 | 0 | 0 | 22 | 100 | 28 |
| –18 | 0 | 0 | 20 | 100 | 15 |
| –21 | 0 | 0 | 28 | 100 | 27 |
| –25 | 0 | 0 | 24 | 100 | 35 |
| –26 | 0 | 0 | 10 | 100 | 11 |
| –27 | 0 | 0 | 16 | 100 | 10 |
| –29 | 0 | 0 | 15 | 100 | 11 |
| –48 | 0 | 0 | 11 | 100 | 16 |
| –51 | 0 | 0 | 5 | 100 | 8 |
| –53 | 0 | 0 | 8 | 100 | 9 |
| –58 | 0 | 0 | 11 | 100 | 16 |
| –65 | 0 | 0 | 8 | 100 | 9 |
| –70 | 0 | 0 | 6 | 100 | 5 |
| –74 | 0 | 0 | 12 | 100 | 16 |
| –88 | 0 | 0 | 2 | 100 | 8 |
| Total breeding true | ..... | ..... | 237 | ..... | ..... |
| 2502 a 1–28 | 1 | 6 | 5 | 41.7 | 9 |
| –40 | 2 | 8 | 9 | 47.4 | 16 |
| –50 | 0 | 9 | 3 | 25.0 | 15 |
| –80 | 1 | 3 | 4 | 50.0 | 17 |
| –90 | 3 | 13 | 3 | 15.8 | 11 |
| Total | 7 | 39 | 24 | 34.3 | ..... |

*Summary*

A summary of the offspring of all $F_1$ and $F_2$ plants which were heterozygous for awning is given in table 13. It will be noted that, while there are certain rather wide deviations from the expected ratio of 3 plants not fully awned to 1 plant fully awned, the total of 3712 individuals gives a very close approximation to this ratio, the deviation being equal to its probable error.

## RELATION BETWEEN PERCENTAGE OF AWNS IN $F_2$ AND PERCENTAGE OF FULLY AWNED PLANTS IN $F_3$

In the course of the studies on awning, the question arose as to whether or not the percentage of awns in $F_2$ bore any relation to the percentage

TABLE 13. SUMMARY OF THE OFFSPRING OF PLANTS HETEROZYGOUS FOR AWNING

| From table | Generation | Awnless | Partly awned | Fully awned | Not fully awned | Fully awned | Ratio per 4 | Deviation | Probable error | Dev. / P. E. |
|---|---|---|---|---|---|---|---|---|---|---|
| 2 | $F_2$ | 172 | 418 | 180 | 590 | 180 | 3.06:0.94 | .06 | .04 | 1.50 |
| 4 | $F_3$ | 266 | 152 | 129 | 418 | 129 | 3.06:0.94 | .06 | .05 | 1.20 |
| 5 | $F_3$ | 192 | 537 | 253 | 729 | 253 | 2.97:1.03 | .03 | .03 | 1.00 |
| 6 | $F_3$ | 104 | 439 | 230 | 543 | 230 | 2.81:1.19 | .19 | .04 | 4.75 |
| 7 | $F_3$ | 170 | 23 | 67 | 193 | 67 | 2.97:1.03 | .03 | .07 | 0.43 |
| 8 | $F_3$ | 90 | 56 | 36 | 146 | 36 | 3.21:0.79 | .21 | .09 | 2.33 |
| 9, 11, 12 | $F_3$ | 29 | 114 | 55 | 143 | 55 | 2.89:1.11 | .11 | .08 | 1.37 |
| Total | ..... | 1,023 | 1,739 | 950 | 2,762 | 950 | 2.98:1.02 | .02 | .02 | 1.00 |

of fully awned plants in $F_3$. In order to show what relation exists between these characters, figure 106 was prepared. In this correlation chart the percentage of awns on the $F_2$ parent is the subject, and the percentage of fully awned plants is relative. The mean for the subject is 45.99, and for the relative 27.68. The coefficient of correlation is $0.30 \pm 0.06$. This is shown graphically in figure 107 by a straight line fitted to the data in figure 106. While the probable error for $r$ is relatively high, it is only about 1/5 of the constant itself. This makes the constant fairly reliable. At the best, perhaps the constant does not show a very strong relation between the two characters. In only three cases of the ten does the percentage of fully awned plants in $F_3$ increase with an increase in the percentage of awns on the $F_2$ parent. There is a low correlation, however, which may be significant.

### RELATION BETWEEN PERCENTAGE OF AWNS IN $F_2$ AND PERCENTAGE OF AWNS ON PARTLY AWNED PLANTS OF $F_3$

In order to show the extent to which the percentage of awns on the $F_2$ parent influences the percentage of awns on the partly awned plants of $F_3$, figures 108 and 109 were prepared. In other words, an answer was sought to the question, Is there a factor, or are there factors, common to certain plants, which tend to regulate the percentage of awns on partly awned plants in each generation? Such an influence might conceivably be brought about either by a modification of the factor for awns in the presence of $I$, or by a regulation of the potency of the $I$ factor either increasing or diminishing its effect on the awning factor.

| Percentage of awns on $F_2$ parent | Percentage of fully awned plants in $F_3$ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1–10 | 11–20 | 21–30 | 31–40 | 41–50 | 51–60 | 61–70 | 71–80 | 81–90 | 91–99 |
| 1–10 | 3 | 2 | 5 | 2 | | | | | | |
| 11–20 | 3 | 3 | 4 | 4 | 2 | 1 | | | | |
| 21–30 | | 4 | 4 | 1 | 0 | 0 | | | | |
| 31–40 | | 2 | 1 | 3 | 1 | | | | | |
| 41–50 | | 5 | 1 | 2 | 0 | | | | | |
| 51–60 | | 3 | 5 | 2 | 1 | | | | | |
| 61–70 | | 3 | 4 | 3 | 0 | 1 | 0 | 1 | | |
| 71–80 | 1 | 1 | 3 | 2 | 1 | 1 | | | | |
| 81–90 | | 1 | 4 | 1 | 6 | 1 | | | | |
| 91–99 | | | 2 | 1 | | | | | | |

$r = 0.30 \pm 0.06$

FIG. 106. RELATION BETWEEN PERCENTAGE OF AWNS IN $F_2$ AND PERCENTAGE OF FULLY AWNED PLANTS IN $F_3$

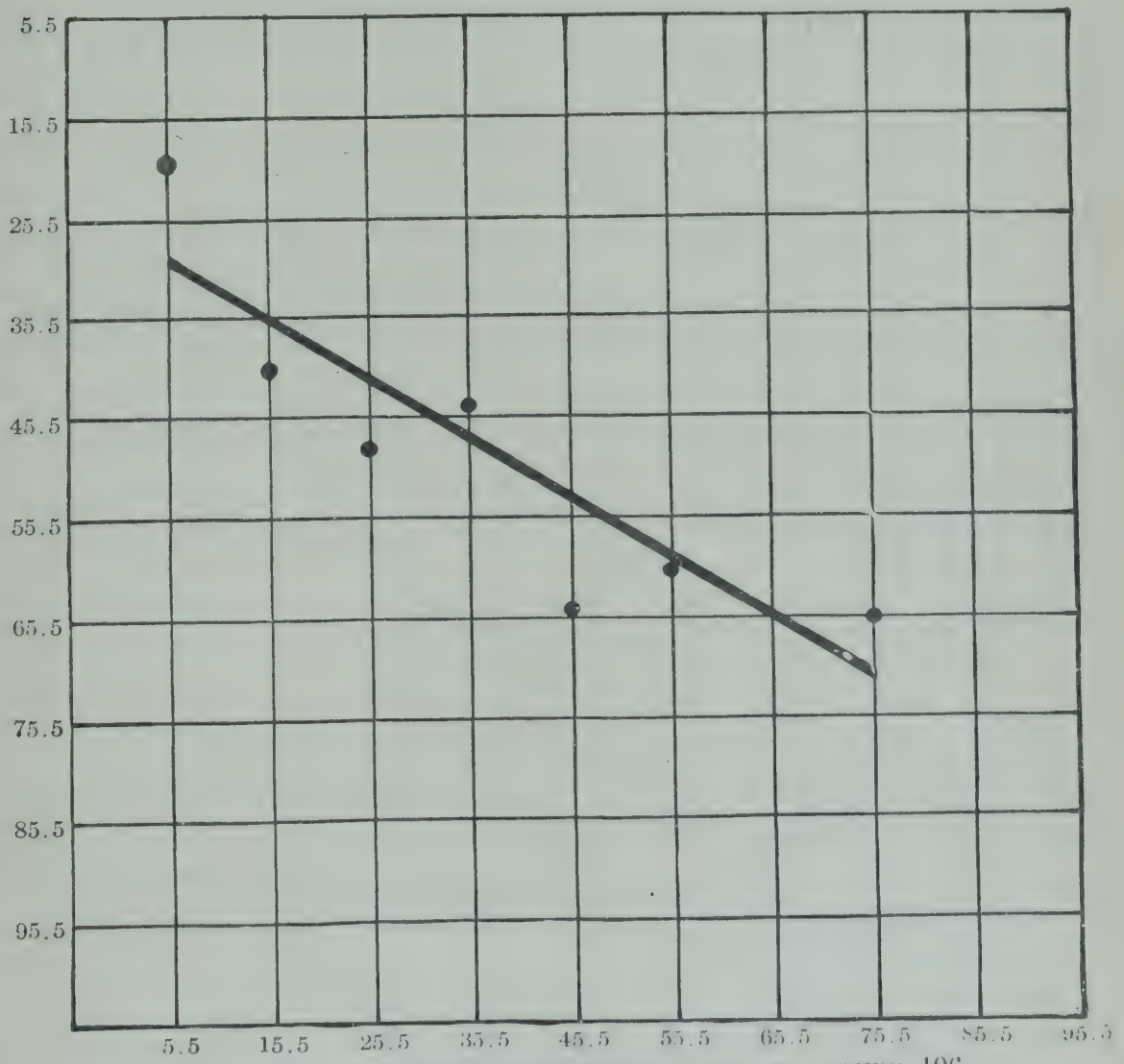


FIG. 107. STRAIGHT LINE FITTED TO DATA IN FIGURE 106

The value of $r$ in this correlation chart is $0.54 \pm 0.05$. The probable error is sufficiently low to make the constant reliable. The coefficient of correlation shows that in about one case out of two there is a general correspondence between the percentage of awns in $F_2$ and $F_3$. In fifty-four cases out of a hundred the percentage of awns on the partly awned plants of $F_3$ is within 10 per cent of the percentage of awns on the parent, which is very significant. Such a correlation in percentage of awns in successive generations may be purely physiological and not dependent on any definite genetic factor. The writer has not been able to ascertain how such a factor behaves in heredity. Possibly it would be very difficult to trace its inheritance because of the fact that much of its influence is probably obscured by the effects of environment on the production of awns.

Nilsson-Ehle (1914:52, table 10) presents data to show the relation between the $F_2$ parent and the $F_3$ offspring with respect to percentage of awns, as follows:

| Frequency of awning of $F_2$ offspring (in per cent) | Frequency of awning of $F_3$ offspring (in per cent) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 0– 10 | 10– 20 | 20– 30 | 30– 40 | 40– 50 | 50– 60 | 60– 70 | 70– 80 | 80– 90 | 90–100 |
| 0– 10 | 45 | 21 | 10 | 10 | | 2 | | | 1 | |
| 10– 20 | | 1 | 6 | 5 | 2 | 1 | | | | |
| 20– 30 | | | 1 | 1 | 7 | 4 | 1 | | | |
| 30– 40 | | | 3 | 5 | 4 | 2 | 2 | 2 | | |
| 40– 50 | | 1 | | 1 | 3 | 2 | 3 | 2 | | |
| 50– 60 | | | | | 1 | | 2 | 4 | 1 | |
| 60– 70 | | | | | | | 3 | 3 | 1 | 1 |
| 70– 80 | | | | | | 2 | 4 | 1 | 1 | 1 |
| 80– 90 | | | | | | | | 2 | 2 | 2 |
| 90–100 | | | | | | 1 | | | | 5 |

$r = 0.85 \pm 0.01$

In this chart are included the awnless and the fully awned plants of both generations. The awnless plants are grouped with plants having less than 10 per cent of awns, and the fully awned plants are grouped with plants having over 90 per cent of awns. The value of $r$ for this table is $0.85 \pm 0.01$. This shows a strong relation between the percentages of awns in the two generations.

| Percentage of awns on $F_2$ parent | Percentage of awns on partly awned plants in $F_3$ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1-10 | 11-20 | 21-30 | 31-40 | 41-50 | 51-60 | 61-70 | 71-80 | 81-90 | 91-99 |
| 1–10 | 1 | 1 | 6 | 2 | 2 | | | | | |
| 11–20 | 5 | 5 | 2 | 5 | | | | | | |
| 21–30 | | 4 | 2 | 3 | | | | | | |
| 31–40 | 1 | 0 | 2 | 2 | 1 | 1 | | | | |
| 41–50 | | | 1 | 4 | 1 | 1 | 1 | | | |
| 51–60 | | 1 | 2 | 0 | 5 | 2 | 1 | | | |
| 61–70 | | | 1 | 4 | 5 | 0 | 1 | 1 | | |
| 71–80 | 1 | 0 | 1 | 2 | 2 | 1 | 2 | | | |
| 81–90 | 1 | 1 | 1 | 2 | 0 | 3 | 2 | 3 | | |
| 91–99 | | | | | 2 | 1 | | | | |

$r = 0.54 \pm 0.05$

FIG. 108. RELATION BETWEEN PERCENTAGE OF AWNS IN $F_2$ AND PERCENTAGE OF AWNS ON THE PARTLY AWNED PLANTS OF $F_3$

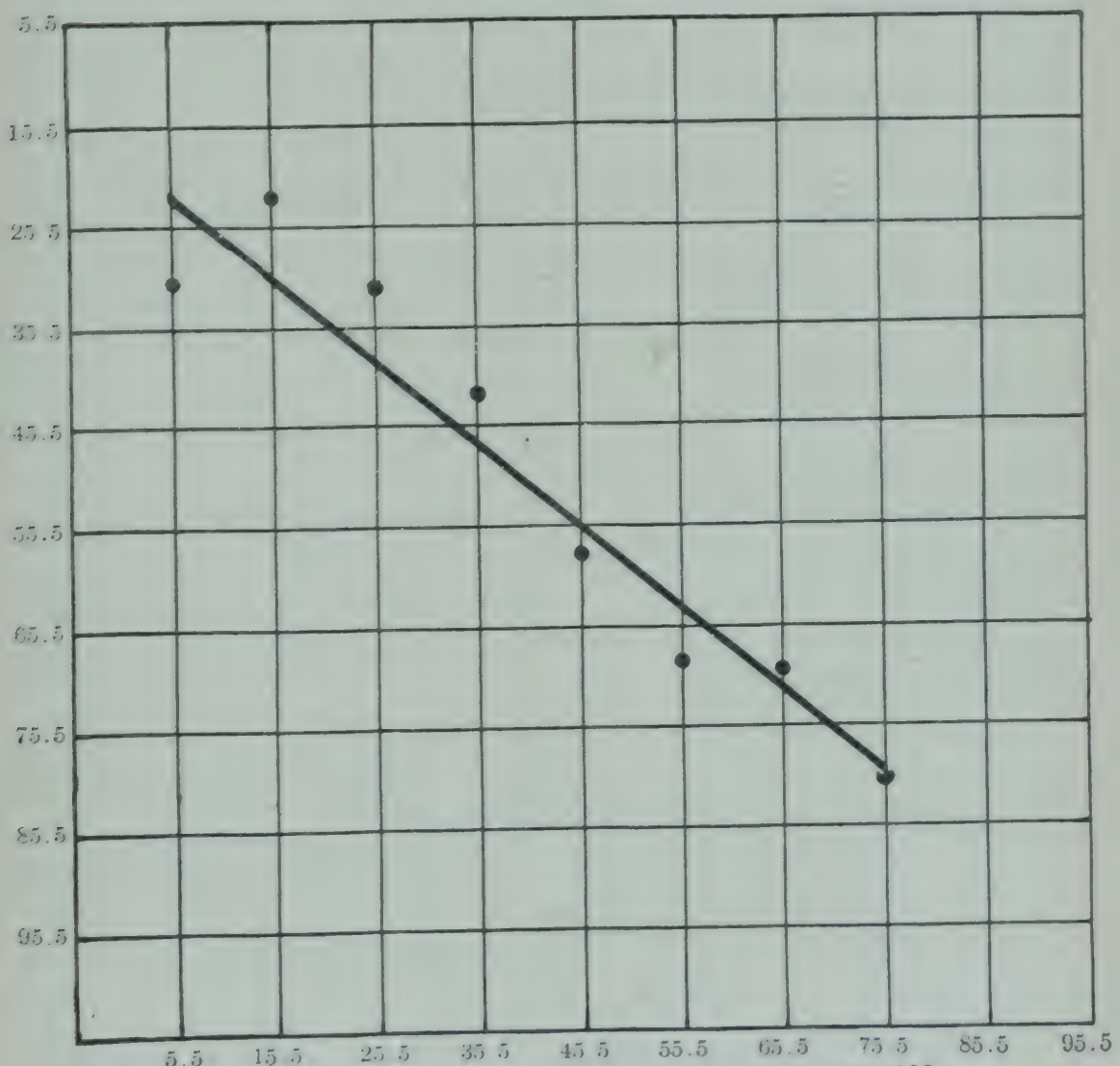


FIG. 109. STRAIGHT LINE FITTED TO DATA IN FIGURE 108

### TWO-AWNED SPIKELETS

Occasionally, in the writer's experiments, spikelets were found having both kernels awned. These two-awned spikelets were found only on panicles that were 100 per cent awned. Plants having 100 per cent of awns did not always have two-awned spikelets, but, as stated above, only fully awned panicles did possess them. There was no regularity of occurrence of these spikelets, and the numbers on different panicles varied greatly. Evidently the two-awned spikelet is produced in the normal expression of the awning factor and in the absence of the inhibitor, *I*. It was never found on partly awned plants, no matter how high the percentage of awns was.

### EFFECT OF ENVIRONMENT ON AWNING

So far as the writer has been able to learn, no experiments have been conducted to determine the effect of environment on the production of awns. It seemed unwise to start such an investigation in connection with these studies until more knowledge was available regarding the factors that govern awning. An experiment of this kind, if conducted with strains of slightly different genetic nature, is of little value.

There is a prevailing opinion among students of inheritance in Avena, that awning in the cultivated varieties is considerably influenced by environmental conditions. Love[3] has said that environment may have a great effect on awns in *A. sativa* but it has no influence on the awns of *A. fatua*. Surface (1916) believes that environment causes certain heterozygous $F_2$ plants to be awnless when they should perhaps be partly awned. Nilsson-Ehle (1914:52) also speaks of the possible effect of environment on awns. None of these writers, however, venture an opinion as to the exact environmental factors that cause awns to increase or decrease in number.

The only facts that can be presented here to answer this question are from a general observation of the crops of different seasons. The crop of 1916 was grown on well-drained soil of good fertility, while the soil on which the crop of 1917 was grown appeared to be less well-drained and was relatively high in nitrogen and organic matter. The data seem to show that there was a greater tendency toward awning in the plants grown in 1916 than in those grown in 1917.

[3] Dr. H. H. Love, in a lecture course in the Department of Plant Breeding, Cornell University, May 11, 1917.

### OCCASIONAL PRODUCTION OF INTERMEDIATE AND STRONG AWNS

It is seen from tables 5 B (page 645) and 6 A (page 647) that there were eighteen series among those studied in $F_3$ which produced either intermediate awns or strong awns, or both kinds. In one case, pedigree 2502 a 1–59, as many as forty-three strong awns and forty intermediate awns appeared. An examination of the $F_2$ data showed that in series 2501 there were 13 plants out of 340 which had either strong awns or intermediate awns, or both, while in series 2502 a 1 there were 2 out of 90 plants which showed this unusual behavior. In no case, either in $F_2$ or in $F_3$, were all the spikelets on a plant awned with either strong or intermediate awns.

Certain of these abnormal $F_2$ plants were propagated for a third generation, in order to see to what extent this condition tended to maintain itself. The results are given in table 14:

TABLE 14. INHERITANCE OF ABERRANT TYPES OF AWNING

| Pedigree | Per cent of $F_2$ awns that were | | Per cent of $F_3$ awns that were | |
|---|---|---|---|---|
| | Strong | Intermediate | Strong | Intermediate |
| 2501 b 1– 49 | 45.0 | 10.0 | 5.24 | 25.24 |
| 54 | 0.0 | 50.0 | 0.0 | 11.11 |
| 64 | 25.0 | 0.0 | 43.0 | 0.0 |
| 117 | 50.0 | 10.0 | 12.5 | 12.5 |
| 2502 a 1– 83 | 0.0 | 15.0 | 6.61 | 14.88 |

All the $F_2$ plants tested gave some awns of the aberrant types in $F_3$. None of them, however, bred true for strong awns or for intermediate awns. Only the tendency to produce such awns was transmitted. In thirteen pedigrees of $F_3$, these abnormal types of awns appeared where none had been present in $F_2$.

The appearance of strong and intermediate awns in the $F_2$ and the $F_3$ progeny of a cross between a weak-awned oat and an awnless variety is indeed difficult to explain. Certain possible explanations are here presented and discussed.

It might reasonably be assumed that these abnormal $F_2$ plants represent natural crosses between strong-awned types and the pedigrees studied,

or between segregates of strong-awned types crossed with cultivated varieties and the pedigrees studied. In the case of the second-generation hybrids such an explanation cannot be given. The first-generation plants were grown in the greenhouse, where natural crossing seldom if ever occurs and where the plants were well separated from others with which they might have crossed. The second-generation plants were grown in the field near certain other oat hybrids. Among the latter were some crosses involving *Avena fatua*, a strong-awned oat. If there were natural crossing in $F_2$, one would expect it to have been with these. Such an event seems unlikely, however, as no clear case of natural crossing in oats has been observed at this station. Furthermore, a cross with *A. fatua* or its hybrids should show other characters of the wild oat besides the strong awn. In only one case was this true, and then only with respect to color and dorsal hairs. The evidence thus seems to be against the theory of a natural crossing.

As a second possible explanation, it might be said that the appearance of scattered spikelets bearing strong or intermediate awns is the result of bud mutation. The idea of mutation, however, carries with it the fact of a perpetuation true to type. It is significant that none of the abnormal grains gave plants in the next generation either with all the spikelets strong-awned or with all having intermediate awns. The $F_2$ plants bred true only for the tendency to produce some strong-awned and intermediate-awned spikelets. In a strict sense, then, this process cannot be considered as bud mutation.

A third possible explanation remains. The aberrant spikelets may represent a reversion or a partial reversion to an ancestral condition. The variety Burt is considered a derivative of *Avena sterilis*. Possibly the reversion is toward this species.

A reversion is generally explained on a Mendelian basis by assuming that certain genetic factors of the wild type have been separated in the course of domestication and have been brought together again by crossing the varieties containing these factors. Reversion in its simplest form involves so-called *complementary factors* which give the return to the ancestral form in the first generation, as in Bateson's cross with sweet peas,[4] in which two strains of white sweet peas gave a purple in $F_1$ when crossed.

[4] Mendel's principles of heredity. By W. Bateson. 1913.

It is not probable, however, that the process of reversion is always as simple as this.

There are at least two ways in which a cultivated variety may arise from a wild species: first, by the loss thru mutation of certain wild characteristics; and secondly, by the obscuring of these characteristics by inhibitors of various sorts. In the event that the wild characters are lost by a process of regressive mutation, they would be expected to reappear only by a reversal of this process. If inhibitors are keeping such characters from expressing themselves, the characters might be expected to appear, either in part or fully developed, when the action of the inhibitor is modified or wholly nullified.

Nilsson-Ehle (1911), in discussing reversion, cites cases which he believes show that some reversions in oats are due to a mutation in certain factors. He believes a change in only one factor of an allelomorphic pair would result in a segregation similar to that which follows hybridizing. Zade (1912), on the other hand, considers these data of Nilsson-Ehle, as well as those of other writers whom he quotes, as failing to show that the reversions discussed were anything more than segregates from natural crosses with the wild types.

As has already been pointed out, there are good reasons for believing that the strong and the intermediate awns have not appeared as a result of hybridization or bud mutation. It seems quite possible that the process is one of reversion, due to a modification of certain inhibitory factors so that they do not completely prevent the appearance of strong awns. For the present, however, such an explanation must be recognized as a conjecture and not as a proved statement of fact.

## BEHAVIOR OF OTHER CHARACTERS

### *Inheritance of basal hairs*

The variety Sixty Day is practically devoid of all hairs at the base of the grain. Occasionally a few basal hairs are present, but these are always short and very sparse. The variety Burt has a dense tuft of hairs at each side of the basal callus. These hairs have been called medium in length in order to allow for certain classes between them and the very short hairs present in some cases on the variety Sixty Day.

On the $F_1$ hybrid between Burt and Sixty Day the basal hairs were somewhat intermediate in length and density between the parental types, but rather strongly inclined toward the condition found in the Sixty Day.

Data on the inheritance of basal hairs in $F_2$ and $F_3$ are given in table 15, which shows the relation between basal hairs and awning. The ratios for each family are given in table 18 (page 665). It is evident from these ratios that the medium type of basal hairs represents the recessive condition. The ratio of basal hairs which are either short or lacking, to

TABLE 15. RELATION BETWEEN BASAL HAIRS AND AWNING

| | Hairs short or none | | Hairs medium long | |
|---|---|---|---|---|
| | Not fully awned | Fully awned | Not fully awned | Fully awned |
| 2501 b 1 | 118 | 4 | 4 | 39 |
| 2501 ar 1 | 77 | 2 | 1 | 26 |
| 2501 ar 2 | 35 | 2 | 1 | 15 |
| 2501 ar 3 | 12 | 0 | 0 | 4 |
| Total 2501–$F_2$ | 242 | 8 | 6 | 84 |
| 2502 a 1–$F_2$ | 67 | 4 | 1 | 18 |
| 2501 –$F_3$ | 813 | 16 | 28 | 275 |
| 2502 –$F_3$ | 525 | 25 | 29 | 200 |
| Grand total | 1,647 | 53 | 64 | 577 |

those which are medium in length, is approximately 3:1. The ratio of the totals, 2.90:1.10, shows a deviation which is nearly four times as great as the probable error. This may seem to be rather high on first consideration, but it must be remembered that, in the case of characters such as this, errors in classification are almost unavoidable. The data clearly point to a monohybrid condition; that is, to a one-factor difference between the two characters.

### *Inheritance of type of base*

The *sativa* and *sterilis* types of basal union, of which the varieties Sixty Day and Burt are examples respectively, have already been described.

In the first generation of the crosses between Burt and Sixty Day the bases of the grains were fairly intermediate in character between the parents. In the $F_2$ the Burt, or *sterilis*, type of base stood out clearly and hence it was compared with the non-Burt types. Data on the $F_2$ and $F_3$ segregates are given in table 16, and the ratios per four are to be found in table 18.

TABLE 16. RELATION BETWEEN TYPE OF BASAL ARTICULATION AND AWNING

| | Non-Burt base | | Burt base | |
|---|---|---|---|---|
| | Not fully awned | Fully awned | Not fully awned | Fully awned |
| 2501 b 1 | 121 | 2 | 1 | 41 |
| 2501 ar 1 | 78 | 1 | 0 | 27 |
| 2501 ar 2 | 35 | 2 | 1 | 15 |
| 2501 ar 3 | 12 | 0 | 0 | 4 |
| Total 2501–$F_2$ | 246 | 5 | 2 | 87 |
| 2502 a 1–$F_2$ | 68 | 5 | 0 | 17 |
| 2501 –$F_3$ | 820 | 19 | 21 | 272 |
| 2502 –$F_3$ | 534 | 25 | 20 | 200 |
| Grand total | 1,668 | 54 | 43 | 576 |

It is apparent that each family gives a close approximation to the 3:1 ratio. The ratio for the totals is fairly close to the expectancy, and its deviation is only slightly more than twice as large as the probable error.

The monohybrid ratio between these two types points to a genetic difference between them of one factor.

*Linkage of medium basal hairs and the fully awned condition*

As the data were being recorded on families 2501 and 2502, it became evident that there was a strong linkage between medium basal hairs and the fully awned condition. Summaries of $F_2$ and $F_3$ series within these families are given in table 15. Of a total of 2341 individuals, 117 were of the cross-over types; that is, there were approximately 5 per cent of cross-overs.[5]

The question may be raised as to whether the factor for medium basal hairs is linked with the factor for complete awning or with the allelomorph of the inhibitory factor, *i*. It seems reasonable to assume a linkage with the awning factor, since the *i* factor is linked with a factor for color, which factor seems to show no linkage with any of the characters that are associated with the fully awned condition.

[5] This method of computing the percentage of cross-overs from the cross-over phenotypes is not exact, of course, since it does not take account of all the individuals that contain cross-over chromosomes. With as small a percentage of crossing-over as is shown here, it gives a figure which is very close to the true percentage. The percentages of crossing-over as they are given here, therefore, are to be considered as only approximately correct.

*Linkage of the Burt type of base and the fully awned condition*

A summary of the data in table 16 shows a strong linkage between the Burt type of base and the factor for complete awning. There were 97 cross-over types out of a total of 2341 individuals, or about 4.14 per cent of cross-overs.

If it is admitted that the linkage of the factor for medium basal hairs is more likely to be with the awning factor than with *i*, then for the same reason this linkage must be assumed to be with the factor for awning. Furthermore, there is a strong linkage between the Burt base and medium basal hairs. If it is assumed that the basal hairs are linked with the awning factor, a similar linkage must be assumed for the Burt type of base.

*Linkage of the Burt type of base and medium basal hairs*

Since there is a linkage between the fully awned condition and both the Burt base and the medium basal hairs, it is evident that there should be a linkage between the last two characters. Such is found to be the case. The data on these two characters are given in table 17, and the ratios per four in table 18. There are 42 individuals of the cross-over types out of a total of 2341, or about 1.79 per cent of cross-overs.

In the accompanying diagram (fig. 110) are shown certain characters

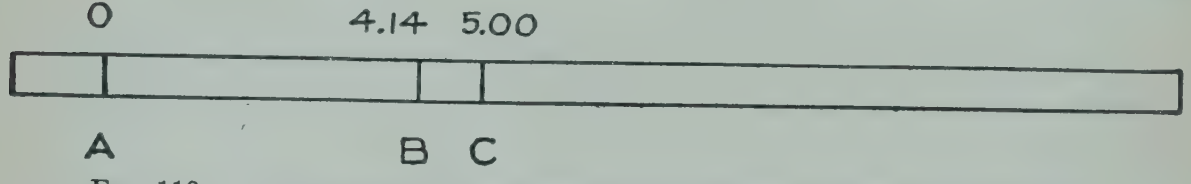


FIG. 110. GROUP RELATION OF CERTAIN CHARACTERS IN THE VARIETY BURT
A, awning factor; B, factor for Burt base; C, factor for medium basal hairs

of the variety Burt which are inherited in group fashion. The relative distances between the factors are based on the percentage of cross-overs. These percentages, of course, can be accepted only as approximately correct, not as indicating the exact distances between the genes on the chromosome. The relations are probably true in a general way. It is apparent that the percentage of crossing-over between the factor for the Burt base and that for medium basal hairs is slightly larger than it should be, based on the relation of these two factors to the factor for awning. The relative positions, however, seem to be correct. In the diagram the factor for awns is arbitrarily placed at zero.

TABLE 17. RELATION BETWEEN TYPE OF BASAL ARTICULATION AND LENGTH OF BASAL HAIRS

| | Non-Burt base | | Burt base | |
|---|---|---|---|---|
| | Hairs short or none | Hairs medium long | Hairs short or none | Hairs medium long |
| 2501 b 1 | 120 | 3 | 2 | 40 |
| 2501 ar 1 | 78 | 1 | 1 | 26 |
| 2501 ar 2 | 36 | 1 | 1 | 15 |
| 2501 ar 3 | 12 | 0 | 0 | 4 |
| Total 2501–$F_2$ | 246 | 5 | 4 | 85 |
| 2502 a 1–$F_2$ | 71 | 2 | 0 | 17 |
| 2501 –$F_3$ | 824 | 15 | 5 | 288 |
| 2502 –$F_3$ | 549 | 10 | 1 | 219 |
| Grand total | 1,690 | 32 | 10 | 609 |

TABLE 18. RATIOS FROM TABLES 15, 16, AND 17 COMPUTED ON THE BASIS OF FOUR

| Pedigree | Basal hairs | | Basal articulation | | Awning* | |
|---|---|---|---|---|---|---|
| | Short or none | Medium | Non-Burt | Burt | Not fully awned | Fully awned |
| 2501–$F_2$ | 2.94 | 1.06 | 2.95 | 1.05 | 2.92 | 1.08 |
| 2502–$F_2$ | 3.16 | 0.84 | 3.24 | 0.75 | 3.02 | 0.98 |
| 2501–$F_3$ | 2.93 | 1.07 | 2.96 | 1.04 | 2.97 | 1.03 |
| 2502–$F_3$ | 2.82 | 1.18 | 2.87 | 1.13 | 2.84 | 1.16 |
| Total | 2.90 | 1.10 | 2.94 | 1.06 | 2.92 | 1.08 |

P. E. for 2341 individuals = ± 0.02

* This table does not include all the data given in table 13. In that table data are given on 3712 individuals, while this summary comprises only 2341.

### *Inheritance of color*

Two colors were concerned in these studies: the red of the variety Burt, and the yellow of the Sixty Day. The two colors were quite distinct in themselves and seemed to afford good subjects for the study of inheritance.

The red of the Burt is not a true red, as one thinks of the color, but rather a dull yellowish red. This seems to be the case with most of the so-called "red" oats. In the Burt, the influence of the yellow element is striking. In the grains that have developed their color poorly, the lemma appears to be a dull yellow or a reddish yellow. The red color, in this case at least, seems to be greatly dependent upon seasonal conditions for its optimum development. Considerable variation in color is to be noted even within the same pure line during different seasons or under strikingly different environmental conditions. There was less variation in the yellow color of the variety Sixty Day, and yet enough to be worthy of mention. When the color was best developed, it was a bright straw yellow. At the other extreme it was a very faint yellow or yellowish.

The $F_1$ between these two varieties was a reddish yellow or a yellowish red, between the shades of color found in the parents.

The second-generation material presented a number of difficulties. The reds and the yellows of the parent types were easily detected, but the intermediate forms were often rather hard to classify. At first an attempt was made to classify the $F_2$ progeny under the colors red, yellow, yellowish, reddish yellow, yellowish red, white, and gray. It soon became apparent that the distinction between reddish yellow and yellowish red was exceedingly fine. There were, however, many individuals which were clearly intermediate in color, and to provide a class for them the reddish yellow class was retained. The gray class was dropped, for reasons which become evident later. The yellowish class included those grains whose color was between yellow and white.

In crosses between blacks and yellows or between blacks and whites, the $F_2$ hybrids are usually rather easy to classify (Nilsson-Ehle, 1909). At least no great difficulties are experienced in classifying them. In such cases there is no overlapping of classes.

In crosses between yellows and whites, Nilsson-Ehle (1909:37–38) found it impossible to distinguish between whites and weak yellows in $F_2$. He declared the $F_2$ frequencies to be of little value, and it was only after a careful study of the third generation that he decided on a 1:2:1 relation between yellows, intermediates, and whites in $F_2$.

So in these studies there was evidently an overlapping of certain classes. It was very hard to draw sharp lines between red and reddish yellow,

or between reddish yellow and yellow, or between yellowish and white, tho the type colors were quite distinct. This trouble in classifying has probably resulted in some unavoidable errors.

The second-generation material was classified for color, and selections of plants having varying percentages of awns were made from each color. It was felt that an $F_3$ from such material would throw light both on the nature of color and on the relation of color to awning. Certain corrections were made in the $F_2$ classification for color as a result of the $F_3$ tests. Notable among these changes was the reduction of the number of whites from 10 to 4 in series 2501. One of the plants classed as white in $F_2$ gave only yellows in $F_3$, two gave only reds, and three gave reddish yellows. The revised data on the $F_2$ of families 2501 and 2502 are given in table 19:

TABLE 19. DISTRIBUTION FOR COLOR OF TWO FAMILIES IN $F_2$

| Color | 2501 | 2502 | Total |
|---|---|---|---|
| Red | 68 | 33 | 101 |
| Reddish yellow | 193 | 38 | 231 |
| Yellow | 33 | 12 | 45 |
| Yellowish | 42 | 7 | 49 |
| White | 4 | 0 | 4 |
| Total | 340 | 90 | 430 |

It is very probable that the reddish yellow class of table 19 contained a number of individuals which were true reds but which failed to develop their color fully. The remainder were undoubtedly either heterozygous for color, or mixtures of red and yellow color. It has seemed advisable to group all the plants containing red into one class. Similarly, the yellowish class probably contained a number of poorly developed yellows. Grouping the data of table 19 as suggested shows the frequencies to be as given in table 20.

The red oat, Burt, undoubtedly contains a factor for red color, or at least a factor that can produce red color when present with some other factor. This factor may be a definite gene for red pigment, or it may represent an intensifier which reacts with the factor for yellow, known to be present in the Burt, to change it to a red. The second generation of families 2501 and 2502 exhibited a well-graded series from light yellow

TABLE 20. A GROUPING OF THE DATA GIVEN IN TABLE 19

| Color | 2501 | | 2502 | | Total | |
|---|---|---|---|---|---|---|
| | Observed | Calculated | Observed | Calculated | Observed | Calculated* |
| Reds | 261 | 254.88 | 71 | 67.68 | 332 | 322.50 |
| Yellows | 75 | 79.65 | 19 | 21.15 | 94 | 100.78 |
| Whites | 4 | 5.31 | 0 | 1.41 | 4 | 6.72 |
| Total | 340 | ..... | 90 | ..... | 430 | ..... |

* Calculated for totals only.

to reds which looked to be even darker than the Burt parent. These gradual transitions from yellow to red suggest a close relation between the two colors. This factor for red, then, may be designated by *R*. It has already been said that the Burt possesses a factor for yellow color. This is apparent from the fact that good yellows appear in crosses of the Burt with Swedish Select or with Early Champion. The last two varieties are white in color (Love and Fraser, 1917:490). The yellow factor carried by the Burt is here represented by *Y*.

The variety Sixty Day obviously lacks the factor for red. Furthermore, the data at hand seem to point to a difference, genetically, between the factor for yellow in the Sixty Day and that for yellow in the Burt, tho both factors seem to produce about the same shade of yellow. The yellow factor in the Sixty Day is here designated as *Y'*.

The genetic formula for the variety Burt, therefore, is *RR YY y'y'*. That for the Sixty Day is *rr yy Y'Y'*. The $F_1$ hybrid has the formula *Rr Yy Y'y'*.

The second generation from such a hybrid contains twenty-seven distinct genotypes, which may be represented in group form by the factors that would tend to express themselves; as

27 *R Y Y'* – red
9 *R Y y'* – red
9 *R y Y'* – red
9 *r Y Y'* – yellow
3 *R y y'* – red
3 *r Y y'* – yellow
3 *r y Y'* – yellow
1 *r y y'* – white

The theoretical ratio in this case is 48 reds:15 yellows:1 white. The calculated frequencies in table 20 are based on this hypothesis.

There are three means of testing the validity of such an hypothesis: first, by comparing the separate frequencies in pairs and applying the probable error; secondly, by computing the closeness of fit, according to the method of Weldon (1901) or that of Harris (1912); and lastly, by growing an $F_3$ and seeing how the $F_2$ plants breed in the next generation. All three tests of this second-generation material have been made, with the following results:

*Testing by probable errors.*— Three tests were applied by the probable-error method, concerning the relation, first, of reds to non-reds, secondly of yellows to non-yellows, and thirdly of whites to non-whites.

In the case of the relation of the reds to the non-reds, a ratio of 3:1 is expected. The probable error is found by the formula

$$E_{no} = \pm 0.6745 \sqrt{0.75 \times 0.25 \times 430}$$

In comparing the yellows and the non-yellows, the formula becomes

$$E_{no} = \pm 0.6745 \sqrt{0.7656 \times 0.2344 \times 430}$$

In comparing the whites and the non-whites the formula is

$$E_{no} = \pm 0.6745 \sqrt{0.9844 \times 0.0156 \times 430}$$

The comparisons of the observed with the calculated results follow:

| | Observed | Calculated | Deviation | Probable error |
|---|---|---|---|---|
| Reds | 332 | 322.50 | 9.50 | ±6.06 |
| Non-reds | 98 | 107.50 | | |
| Yellows | 94 | 100.78 | 6.78 | ±5.93 |
| Non-yellows | 336 | 329.22 | | |
| Whites | 4 | 6.72 | 2.72 | ±1.73 |
| Non-whites | 426 | 423.28 | | |

In each of the above cases the deviation is considerably less than twice the corresponding probable error. This indicates a fairly good agreement between observed and calculated results, and lends plausibility to the hypothesis stated above.

*Closeness of fit of color data.*— When the closeness of fit is calculated according to the method of Weldon (1901) or that of Harris (1912), the value of $\chi^2$ is found to be 1.8367. This gives to $P$ a value of 0.406851. With a perfect fit, the value of $P$ would be 1.00. The value 0.406851 indicates a fairly good fit, since it points to the probability of deviations as great as those obtained occurring four times out of ten; that is, in four cases out of ten such deviations are to be looked for in random samples. Were it not for the high value of $\frac{(o-c)^2}{c}$ which accompanies the whites, the fit would be even better. This deviation among the whites is not excessive, however, and the fit can be accepted as a good one.

| | Observed | Calculated | (o-c) | $(o-c)^2$ | $\frac{(o-c)^2}{c}$ |
|---|---|---|---|---|---|
| Reds | 332 | 322.50 | +9.50 | 90.25 | 0.2798 |
| Yellows | 94 | 100.78 | —6.78 | 45.97 | 0.4561 |
| Whites | 4 | 6.72 | —2.72 | 7.398 | 1.1008 |

$$\chi^2 = 1.8367$$

*Test of the $F_2$ in $F_3$.*— The best test of the validity of any theory regarding a second generation of plant hybrids is to grow pedigree cultures of the different types of $F_2$. A test of this nature is of great value where it can be made with accuracy. In the case of the material examined here, however, such a test is open to certain objections. In the first place, the $F_2$ material was not analyzed in detail because of the great difficulty of making a distinction between the various shades of closely related colors. An $F_2$ plant chosen for test, therefore, was classed only as a red, a reddish yellow, a yellow, a yellowish, or a white, and the burden of the test as to its factorial constitution fell entirely upon the third generation.

The cultures in $F_3$ were limited in size, partly by the desire of the investigator to study a large number of pedigrees, and partly by the fact that in many cases the number of seed from one panicle was rather small. The information supplied by the $F_3$, then, is of a general nature. For example, it tells how many $F_2$ reds are breeding true and how many are segregating, without telling which ones give a 3:1 ratio and which a

48:15:1. Such information, however, furnishes a test of the second generation as it was analyzed. The results of this test are shown in table 21:

TABLE 21. BEHAVIOR OF $F_2$ PLANTS IN $F_3$

| Color | Pedigree 2501 | | Pedigree 2502 | | Total number | |
|---|---|---|---|---|---|---|
| | Plants breeding true | Plants segregating | Plants breeding true | Plants segregating | Plants breeding true | Plants segregating |
| Red | 11 | 10 | 11 | 22 | 22 | 32 |
| Reddish yellow | 11 | 29 | 9 | 28 | 20 | 57 |
| Yellow | 15 | 7 | 6 | 6 | 21 | 13 |
| Yellowish | 8 | 18 | 2 | 6 | 10 | 24 |
| White | 4 | 0 | 0 | 0 | 4 | 0 |

It was to be expected that a large number of the $F_2$ reds would be homozygous for the *R* factor and would therefore breed true. Similarly, a large proportion of the $F_2$ reddish yellows might be expected to be heterozygous for *R* and to break up. Both these facts are borne out by table 21. From the theory propounded above, one-third of the red plants should breed true in $F_3$ and the remainder should break up. The table shows that 42 reds of $F_2$ bred true in $F_3$, and 89 broke up.

By the same theory 7 yellows should breed true and 8 should break up. From the table it is seen that 31 yellow or yellowish bred true, and 37 broke up. The expectancies are 32.2 of the sort which breed true to 36.8 of the others.

The whites of $F_2$ are undoubtedly triple recessive. The four whites of $F_2$ gave nothing but whites in $F_3$.

In certain $F_2$ and $F_3$ cultures there appeared dark brown oats, somewhat similar in color to the grains of *Avena fatua*. In the case of the first brown that appeared, the brown color was associated with some strong awns and the plant was discarded as a possible mixture or even a natural hybrid with the wild types. The remainder of the browns appeared in $F_3$. These very evidently possessed characters of the species *A. sativa* and *A. sterilis*. As there were no plants of *A. sterilis* near either the $F_1$ or the $F_2$ hybrids studied here, these brown oats must be looked upon as having come from the original cross of Burt x Sixty Day. No fourth

generation has as yet been grown, and so it is impossible to say how these brown grains behave in heredity. They probably are the result of mutation, tho the process of reversion might well produce such grains.

Certain plants in $F_2$ bore grains which showed a gray color very distinctly. In some cases this color was well developed, so that the whole grain might have been spoken of as gray; in others the gray was present only as a very light wash or stripe over a ground color of red or yellow; in still other pedigrees there was a very faint suggestion of gray and its presence was very doubtful. There was no regularity in the occurrence of these grays in the different families, nor did their frequencies agree with any plausible theory of color inheritance. It seems probable that the $F_2$ grays do not tell the whole truth regarding the gray color.

Certain of the $F_2$ grays bred entirely true in $F_3$, but most of them gave only reds and yellows. Other pedigrees which had shown no gray color in $F_2$ developed gray in $F_3$. It was almost impossible to decide on the true number of grays in the second generation. Evidently gray is influenced to a marked extent by external factors. Nilsson-Ehle (1909) found that soil and seasonal conditions affected the expression of gray color to a considerable degree. As far as possible in these studies, the grays were grouped under the color which appeared to be associated with the gray, as red or yellow.

The exact source of the gray is, for the present at least, a matter of conjecture. It may be developed by the union of complementary factors, one from each parent. Or it may be called into expression by the interaction of a number of factors.

Nilsson-Ehle (1914) reports a yellow oat, a strain of the variety Probsteier, in which the yellow color either inhibits the formation of awns or carries with it a closely linked factor which functions in the same manner. Surface (1916), in a cross between the species *Avena fatua* and the *A. sativa* variety Kherson, presents data which seem to show that the Kherson carries a factor similar to that in the yellow Probsteier. Love and Fraser (1917) report that the yellow of the variety Sixty Day apparently carries a factor which inhibits awning. Love and Craig (1918) present data to show that the Sixty Day does carry such a factor, and that this factor definitely inhibits the production of awns by $F_2$ yellows in a cross with *A. fatua*.

The effect of the inhibitor in these investigations is evidently obscured by the presence in the Burt of a factor for yellow which lacks the inhibitor. It can be seen from table 22 that there is no striking influence of an inhibitory factor to be detected in the yellow grains of $F_2$. It is true that 55 of the $F_2$ yellow plants have less than 50 per cent of awning, while only 39 lie at the other half of the table, but this is not particularly striking. The yellow factor in the Burt has been shown in previous crosses (Love and Fraser, 1917:490) to lack the inhibitory factor. The fully awned yellows of table 22, and most of the partly awned yellows, are probably the Burt yellows.

TABLE 22. RELATION BETWEEN COLOR AND AWNING IN TWO $F_2$ FAMILIES

| Color | Percentage of awns | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1–10 | 11–20 | 21–30 | 31–40 | 41–50 | 51–60 | 61–70 | 71–80 | 81–90 | 91–99 | 100 | Total |
| Red | 12 | 13 | 12 | 7 | 5 | 9 | 6 | 3 | 6 | 5 | 3 | 20 | 101 |
| Reddish yellow | 30 | 22 | 15 | 13 | 14 | 19 | 14 | 13 | 5 | 13 | 4 | 69 | 231 |
| Yellow | 10 | 4 | 1 | 3 | 4 | 3 | 1 | 3 | 1 | 4 | 0 | 11 | 45 |
| Yellowish | 8 | 9 | 7 | 2 | 1 | 3 | 1 | 3 | 1 | 0 | 0 | 14 | 49 |
| White | 2 | ... | ... | ... | ... | 2 | ... | ... | ... | ... | ... | ... | 4 |
| Total | 62 | 48 | 35 | 25 | 24 | 36 | 22 | 22 | 13 | 22 | 7 | 114 | 430 |

## SUMMARY

Certain conclusions can be drawn from the foregoing data. An enumeration of these follows.

1. In a cross between the Burt, which is fully awned, and the Sixty Day, which is awnless, there is a nearly complete dominance of the awnless condition.

2. From certain facts to be observed in the preceding tables, it seems probable that both parents contain the factor for awning but that it is prevented from operating in the variety Sixty Day by an inhibitor which is closely linked with the factor for yellow color in that variety.

3. The production of awnless or partly awned plants in the first generation is dependent on the extent to which this inhibitor, *I*, is dominant over its normal allelomorph *i*. This dominance is probably dependent to a large extent on environmental factors.

4. In the second generation, awnless, partly awned, and fully awned

plants are produced in approximately the ratio of 1:2:1. The ratio of plants not fully awned to plants fully awned is very close to 3:1.

5. A third-generation test of $F_2$ plants shows that the fully awned plants are pure recessives and that they breed true for 100 per cent of awns.

6. A test of the partly awned plants shows that nearly all these plants are heterozygous, since they give in $F_3$ approximately three plants not fully awned to one that is fully awned; that is, they duplicate the behavior of the $F_1$ plants. The formula for these plants would be *Ii*. A few partly awned plants of the second generation, which had a very low percentage of awns, were found to really belong to the awnless class. The appearance of awns on these plants is probably due to a slight modification of the action of the inhibitory factor, perhaps by environmental influences.

7. The awnless $F_2$ plants were found to consist of two types genetically: those plants which bred true, or practically so, for the awnless condition, and those which gave a segregation like that given by an $F_1$ plant. The formula for the first would be *II*, and for the second *Ii*.

8. Spikelets having two awns, one on each kernel, are to be found only on plants having all the spikelets awned. The irregular occurrence of such two-awned spikelets makes it seem likely that there is no definite genetic factor involved, but rather that it is the natural behavior of the awning factor to produce two awns occasionally in the absence of the inhibitory factor.

9. Environment seems to affect the production of awns to a considerable extent. While experimental evidence is wanting, general observation suggests that an increase in the moisture content of the soil and of its organic matter and nitrogen tends to decrease the number of awns.

10. Strong and intermediate awns appear in small numbers on a few of the $F_2$ plants and in about the same relative numbers on the $F_3$ progeny of these plants, as well as on the progeny of certain other $F_2$ plants which bear only weak awns. Such a phenomenon may be due to a reversion of a complex nature.

11. There is a strong linkage between the fully awned condition and the medium long hairs at the base of the grain. In 2341 individuals there were about 5 per cent of cross-overs.

12. A similar linkage exists between the fully awned condition and the Burt (similar to *Avena sterilis*) type of basal articulation. Here there were practically 4.14 per cent of cross-overs among 2341 individuals.

13. The non-Burt type of basal articulation is dominant over the Burt type in $F_1$. The $F_2$ gives three non-Burt plants to one Burt.

14. Short basal hairs or no basal hairs are dominant over those which are medium long. The $F_2$ ratio is three of the former to one of the latter.

15. Two colors are contrasted — a red or a yellowish red of the variety Burt, and the clear yellow of the Sixty Day.

16. The $F_1$ plants are intermediate for color.

17. The $F_2$ presents certain difficulties. Its colors are greatly influenced by external factors, and they grade into one another in a manner to make a perfect classification practically impossible.

18. The Burt oat possesses a factor for red color, and a factor for yellow which is distinct from the Sixty Day factor and which carries no inhibitor to awning. The genetic formula for the variety Burt would be $RR\ YY\ y'y'$.

19. The variety Sixty Day would have the genetic formula $rr\ yy\ Y'Y'$.

20. The $F_2$ data on color agree rather closely with the theory as to the genetic constitutions of the two parents. The ratios in two families are close to 48 reds: 15 yellows: 1 white.

21. The third-generation tests bear out this theory in a general way.

22. A few brown grains appeared in the course of these studies. They may be the result either of mutation or of reversion.

23. Other workers have shown that the variety Sixty Day carries with it a factor which inhibits the production of awns, which factor is closely linked with the factor for yellow color. Because of the yellow in the variety Burt, which carries no inhibitor, the inhibitory effect of the Sixty Day factor was obscured.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# A STUDY OF THE PLANT LICE INJURING THE FOLIAGE AND FRUIT OF THE APPLE

ROBERT MATHESON

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# A STUDY OF THE PLANT LICE INJURING THE FOLIAGE AND FRUIT OF THE APPLE

# A STUDY OF THE PLANT LICE INJURING THE FOLIAGE AND FRUIT OF THE APPLE

ROBERT MATHESON

Three species of plant lice — the green apple aphis, *Aphis pomi* De Geer (*Aphis mali* Fabricius), the rosy apple aphis, *Aphis sorbi* Kaltenbach, and the grain, oat, or apple-bud aphis, *Aphis avenae* Fabricius — are frequently very injurious to the foliage and fruit of apple. Of the three species the green apple aphis is undoubtedly the most common and widespread, doing considerable injury every year not only in bearing orchards but also in young orchards recently set and in nurseries. The greater amount of injury wrought by this species is due to the fact that it remains on the apple tree thruout the season, whereas the rosy aphis and the apple-bud aphis, or grain aphis, migrate in May, June, and early July to other host plants. In recent years the rosy aphis has also become very injurious and it now probably does as much damage in bearing orchards as does the green aphis, if not more.

## DISTINGUISHING CHARACTERS OF THE THREE SPECIES OF APHIDS

The three common aphids on the apple can be readily separated in all the stages of their complicated life histories. From the standpoint of the grower it is most essential that he recognize the species as soon as they appear in the spring. The first nymphal stages of the stem mothers can be separated readily both on color markings and on structural characters. These characters may be tabulated as follows:

| Species | Color | Structural characters |
|---|---|---|
| *Aphis pomi* De G..... | Dark apple green..... | Cornicles cylindrical, about as long as a body segment; unguis equal to one-half length of segment. |
| *Aphis sorbi* Kalt..... | Dark green, with a double row of black spots down the dorsum; sides with distinct white pulverulence. | Cornicles long, cylindrical, flanged at tip; unguis distinctly twice as long as base of last segment. |
| *Aphis avenae* Fabr..... | Dark yellowish green..... | Cornicles very short, tuberculate: unguis distinctly longer than one-half of segment. |

The distinguishing characters mentioned in the table are well shown on Plate XVIII and in figure 111. In the field these can be seen readily with the aid of a hand lens.

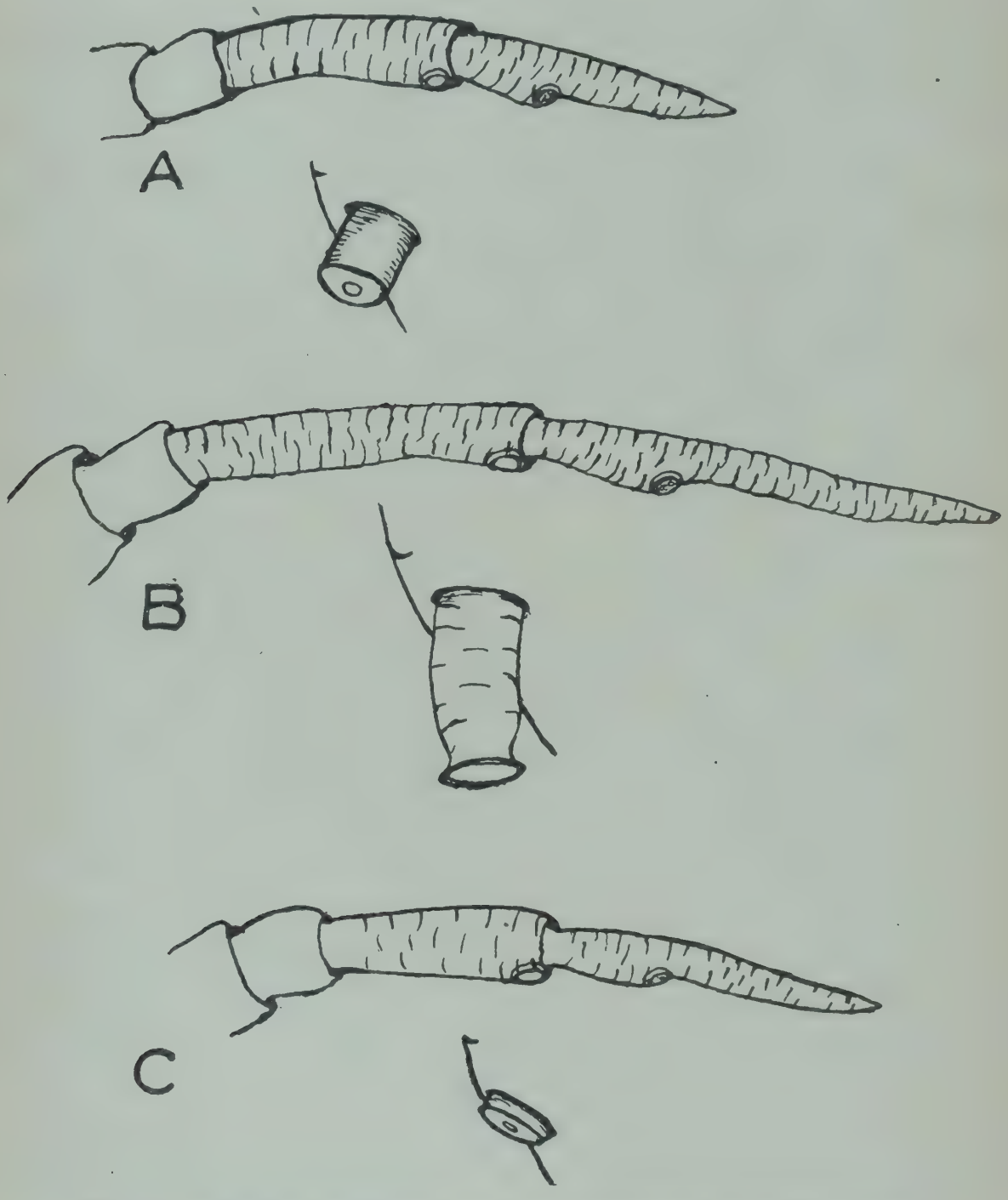



FIG. 111. ANTENNAE AND CORNICLES OF FIRST INSTAR OF STEM MOTHERS
A, *Aphis pomi*; B, *A. sorbi*; C, *A. avenae*. All drawn to same scale

The mature stem mothers are more easily separated than are the nymphs, tho the color markings vary considerably with each species. The typical forms, drawn to the same scale, are shown in Plates XIX–XXI, and the antennæ in figure 112.

*Aphis pomi* undergoes very slight changes in color. The mature stem mother is bright yellowish green (Plate XIX). The head is brownish,

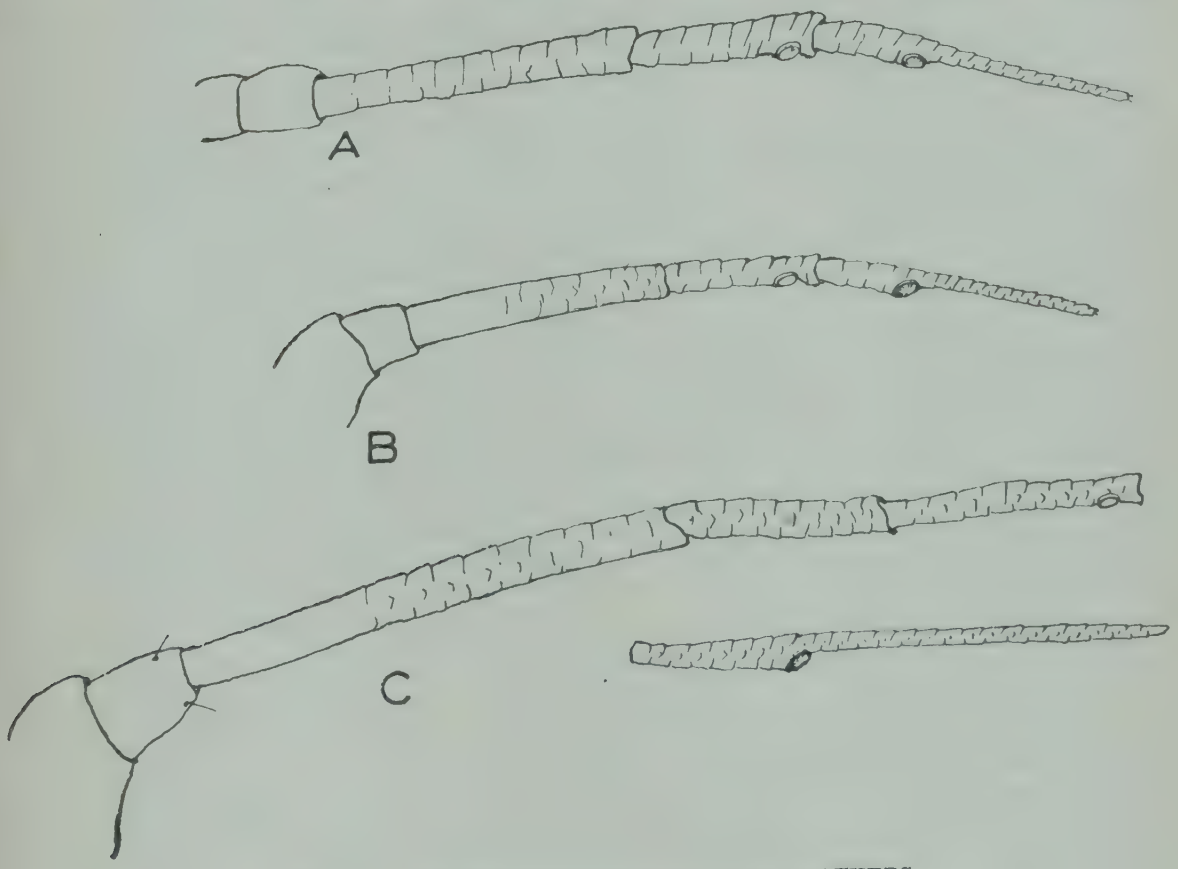



FIG. 112. ANTENNAE OF MATURE STEM MOTHERS

A, *Aphis pomi*; B, *A. avenae*; C, *A. sorbi*. All drawn to same scale

tending toward almost black in some cases. The cornicles, the tips of the antennae, and the cauda are black, showing in marked contrast to the remainder of the body.

*Aphis sorbi* varies considerably in color markings. The typical form is shown in Plate XX. The color is generally a purplish brown, intermingled with greenish on the dorsum. The whole body is covered with a fine white pulverulence. There is generally a reddish brown area between the bases of the cornicles. The cornicles and the antennae, except the basal segments, are black.

*Aphis avenae* is very characteristic in color and is easily identified. It is yellowish green, with a dark green band extending the full length of the abdomen. This band is expanded laterally at the base of each segment, as shown in Plate XXI.

## THE GREEN APPLE APHIS

## (*Aphis pomi* De Geer)

### SYNONYMY

The green apple aphis is a European insect. When and where it was introduced into America will in all probability never be definitely known. Unfortunately European writers have so confounded this species with the other two common plant lice of apple that it is extremely difficult, and in many cases impossible, to determine which insect is under discussion. Frequently in the same article the three well-marked species are described as if they were identical. Owing to this confusion American writers have, until recent years, failed to correctly identify the species under discussion, and the literature is in a sadly confused state. In order to clarify the situation, the following synonymical bibliography should be of considerable value:

1773 *Aphis pomi* De Geer, Mém. 3:53, pl. 3, figs. 18–21.
1775 *Aphis mali* Fabricius, Syst. Ent., p. 737, no. 19.
1794 *Aphis mali* Fabricius, Ent. Syst. 4:216, no. 29.
1802 *Aphis pomi* Vallot, Conc. Syst. Ouvr. Réaumur, p. 95.
1803 *Aphis mali* Fabricius, Syst. Rhyng., p. 298, no. 29.
1837 *Aphis pyri mali* Schmidberger, Köllar's Ins. Inj. Gard., For., and Farmers.
1843 *Aphis mali* Kaltenbach, Mon. Fam. Pflanzenläuse, p. 72.
1850 *Aphis mali* (in part) Walker, Ann. and Mag. Nat. Hist. 2:5:269.
1851 *Aphis mali* (in part) Fitch, Cat. Ins. Cab. Nat. Hist., p. 65.
1855 *Aphis mali* (in part) Fitch, Trans. N. Y. State Agr. Soc. 14:753.
1856 *Aphis mali* Fitch, Trans. N. Y. State Agr. Soc. 16:333.
1857 *Aphis mali* Koch, Die Pflanzenläuse, p. 107.
1863 *Aphis mali* Passeirni, Aphidae Ital.
1868 *Aphis mali* Walker, The Zoologist, p. 1297.
1871 *Aphis mali* Taschenberg, Ent. f. Gärtner und Gartenfreunde, p. 465–466.
1879 *Aphis mali* (in part) Buckton, Mon. Brit. Aphides 2:44–50.
1880 *Aphis mali* Taschenberg, Prakt. Ins. Kunde, pt. 5:53–55.
1887 *Aphis mali* (in part) Oestlund, Syn. Aphididae Minn., p. 64.
1900 *Aphis mali* Smith, N. J. Agr. Exp. Sta., Bul. 143.
1900 *Aphis mali* Smith, Ent. News 11:448.
1901 *Aphis padi* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. 12:191–192.
1902 *Aphis pomi* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. 13:130–136.
1904 *Aphis mali* Pergande, U. S. Div. Ent., Bul. 44:5.

HISTORICAL

To determine when this plant louse was brought to America has been impossible because of the confused state of the literature. Due to the statements of Pergande (1904)[1] it has been generally held that the species is of recent importation. Pergande, in a careful study of *Siphocoryne* (*Aphis*) *avenae* Fabr., endeavors to clarify the synonymy of that species and concludes that it is identical with *Aphis mali* Fitch *nec* Fabricius. He states that the true European apple louse, *Aphis mali* De Geer (he surely means *Aphis pomi* De Geer, or *Aphis mali* Fabricius), was first observed by himself in the spring of 1897 and has since spread thruout the United States. That he was mistaken in his conclusions can be readily shown by a careful reading of literature.

Fitch (1855 a) in his first report has undoubtedly confused *Aphis avenae* Fabr. and *Aphis pomi* De G. This is shown in his descriptions of so many varieties, in his summary of the life history of the species, and furthermore in his published notes in the *Country Gentleman* (Fitch, 1855 b) and in his illustrations and notes in his third report (Fitch, 1856). In the *Country Gentleman* he inserts a letter from William Gilchrist, one of his correspondents, who reports on June 25, 1855, myriads of plant lice infesting his young orchard. These lice were injuring young fruit, were curling the leaves severely, and were congregated in great numbers on the tender twigs. Such are not the habits of *Aphis avenae* Fabr. (*Aphis mali* Fitch), and Dr. Fitch was puzzled, as is shown in his comments on the letter. Fitch's early observations had been confined to an infestation of *Aphis avenae* Fabr., with which were undoubtedly mingled some *Aphis pomi* De G. Evidently the injury reported by Gilchrist was caused by *Aphis sorbi* Kalt. or *Aphis pomi* De G. or by both species. In his discussion of the life history Fitch certainly outlines that of *Aphis pomi* De G. If he did not copy the life history in its entirety from European authors, he must have made some observations which warranted such an accurate description of many of the activities of *Aphis pomi* De G. Fitch also records the observations of Gilchrist that Northern Spy and Red Astrachan are not so susceptible to attack as are other varieties. This is in agreement with the recorded experience of entomologists with reference to *Aphis pomi* De G.

[1] Dates in parenthesis refer to Bibliography, page 760.

Further evidence that Fitch has undoubtedly confused *Aphis avenae* Fabr. with *Aphis pomi* De G. is seen in his third report. Figures 1 and 5 on Plate I certainly do not represent *Aphis avenae* Fabr. but are clearly illustrations of *Aphis pomi* De G. His notes also describe the work of the latter species.

It would seem to the writer that Fitch in his first detailed account confused the two species, tho undoubtedly *Aphis avenae* Fabr. was the more abundant that season and consequently Fitch's descriptions are taken from specimens of that species. However, one or more of his varieties are undoubtedly *Aphis pomi* De G., but it is difficult to definitely decide which.

If this diagnosis of the facts is correct, *Aphis pomi* De G. undoubtedly occurred in America earlier than 1854. The species doing so much injury to the young orchard of Colton (1855) in Vermont were, judging from the description of their work, probably *Aphis pomi* De G. and *Aphis sorbi* Kalt., tho it might be possible that only one species was present. Colton reports the work of these lice to have been severe since 1849. The work is certainly not that of *Aphis avenae* Fabr., and it must be concluded that either *Aphis pomi* De G. or *Aphis sorbi* Kalt. was the offender or that both species were present. This would give 1849 as the first year in which the species was recorded as doing serious injury to young apple trees in the eastern United States.

Undoubtedly the three species of plant lice, *Aphis pomi* De G., *Aphis sorbi* Kalt., and *Aphis avenae* Fabr., which are now common on apple thruout the greater part of the United States and Canada, came here from Europe in the first half of the nineteenth century. The first records of severe injury to apple are from Vermont in 1849, this injury being undoubtedly due, in part at least, to the work of *Aphis pomi* De G. Such a record would indicate that this plant louse had been present for some considerable time. Unfortunately nearly all the entomologists have confused these three species, and it is only by the most painstaking effort that it has been possible to offer the tentative synonymical table appearing on page 686. The writer feels confident that this species has been in America since the middle of the preceding century, tho it was not definitely identified until 1897.

Conclusive evidence that this species was present and widely distributed before 1897 is found in the preservation of specimens in Monell's

collection. This consists of a winged female and several young collected in St. Louis, Missouri, on July 4, 1877. Monell has the following note of this collection: "The aphids on green twigs and under side of leaves of June apple in back garden (Shaw's Garden, St. Louis, Mo.) July 4, 1877. Winged specimens under lens with abdomen green, head and thorax black; honey tubes dark; the apterous have abdomen green and thorax and head green; honey tubes black."[2]

Further evidence that the species had been present for a long time is shown by its wide distribution at the time (1897) of its first positive identification. It was found in New Jersey in 1897, in Colorado in 1898 (Professor Gillette informs the writer by letter that there are specimens in his collection bearing that date), and in Delaware in 1900.

## NATURAL HISTORY

Altho the species *Aphis pomi* has been present in Europe for centuries, no very satisfactory account of its life economy can be found in European literature. While Réaumur (1734-42) mentioned plant lice as curling the leaves of apple, he gave no clear, concise description of this species or its work. De Geer (1752-78), in his remarkable Mémoires, gives a more detailed account of this species, applying to it for the first time the name *Aphis pomi*. De Geer did not confuse this species with the other two, and he presents a clear, concise account of its life history on the apple. Unfortunately this account did not attract the attention of the European entomologists, so that even to the present day the accounts of the plant lice on apple are most confused. This is all the more notable as the three common species of plant lice on the apple differ so remarkably in their life histories, their activities, and the character of their injuries to the foliage. Pergande (1904) was the first entomologist in America to clearly distinguish this species, and Smith (1900 a) was the first to present a concise account of its life history under the name *Aphis mali* Koch. Sanderson (1902) recognized that the species *Aphis mali* described by Smith is the true *Aphis pomi* De Geer. Sanderson also recognized the other two common species of apple plant lice and gave a connected account of the three species. Since the present manuscript was

[2] This information was furnished the writer by J. J. Davis, who has recently studied the Monell collection and who sent the writer the specimens referred to above.

prepared there have appeared two good biological accounts of this aphis, one by Brittain (1915 b) and the other by Baker and Turner (1916 a.)

The green apple aphis is the only species of plant lice which spends its entire life on the apple tree. This was shown by De Geer in 1773, but for some reason his interesting account remained unknown until within very recent years. The winter is passed in the egg stage. The eggs are found scattered over the succulent twigs and branches, usually in cracks or crevices or around the base of fruit spurs or leaf buds; in fact eggs may be found on almost any part of the branches when the lice are very abundant.

### *Hatching of the eggs*

The eggs (Plate VII) hatch early in the spring, about the time when the flower buds show green at their tips or just a little later. The exact date on which the eggs began hatching at Ithaca in 1915 was April 21. This record is for eggs of this species which were laid the preceding autumn on seedling apple trees in rearing cages. These trees were kept caged all winter under normal outdoor conditions. On April 22 hatching became more general, the lice appearing in great numbers. On the 26th, large numbers of the eggs were hatching and the first cast skins were found. This continued for several days, the last eggs on this tree hatching about May 1. It will thus be seen that for this species the eggs hatch over a considerable period, at least ten days in the case of the caged trees. From observations made under orchard conditions similar conclusions were drawn, the eggs hatching during a period of at least ten days. However, the majority of the eggs hatch during the first few days, that is, at the time when the flower buds are showing green. The number of eggs hatching after the first four or five days is not very large, but this depends much on weather conditions. Sudden cold weather may delay hatching or it may destroy the young lice before they leave the eggs. In the spring of 1916 eggs were observed hatching when the blossom buds showed pink, a very important consideration when the problem of control is taken into account.

These observations are in agreement with those of other workers. Smith (1900 a) found the hatching period in New Jersey to extend over at least fifteen days (from April 15 to April 30). Gillette and Taylor (1908) state that in Colorado the eggs begin hatching before the apple

buds show green, and continue hatching for a period of two or three weeks depending on weather conditions. Brittain (1915 a) reports the remarkable observation that on different varieties of apples the eggs hatch at the time when the buds on such varieties are showing green. If such an observation should prove correct for other sections of the country, it would certainly be rather remarkable, to say the least.

### *Failure of the eggs to hatch*

That many, in fact a very large proportion, of the eggs do not hatch, has been observed by many workers. Tho hundreds and thousands of eggs may be found on individual trees, it often happens that only comparatively few of these hatch; so that predictions as to outbreaks of plant lice cannot be made from any examination during the dormant season. Various reasons have been assigned for this failure of eggs to hatch, but none of the factors involved have been given sufficient study, particularly under experimental conditions. Unfortunately the writer has not been able, thru lack of equipment, to do more than make field observations, record the percentages of eggs that hatched, and in general correlate observed phenomena, in so far as possible, with any or all of the factors involved.

The following factors have generally been assigned as contributing to the failure of eggs to hatch:

1. Climatological conditions. These may be (1) temperature — either low temperature or sudden changes during the winter or during the hatching period; or (2) moisture — cold rains just at or just before hatching time, causing the death of the young lice before leaving the eggs.

2. Various predacious insects and birds, which may destroy or injure large numbers of the eggs during late fall, winter, and early spring.

3. Non-fertilization of the eggs. This factor, not yet mentioned by any worker, may account for the failure of many eggs to hatch. All observers agree that the males are very few, constituting a very small proportion of the total number of insects. In cage studies many females were observed to deposit eggs, thousands in fact, and tho these eggs were given the best of conditions the majority failed to hatch. It was observed also that many females deposited eggs before mating, and in a very short time shrunken eggs were noted on the twigs. Whether non-

fertilized eggs of this species will over-winter and hatch in the following spring has not been determined.

As to the proportion of the eggs that actually hatch, no very definite data can be given, as most workers content themselves with general statements. Gillette and Taylor (1908) report that in eastern Colorado not over one per cent of the eggs hatch. Brittain (1915 a) reports, in his work in Nova Scotia, 11.5 per cent hatching, and he states that other workers record as high as 30 per cent. Tho these statements refer to *Aphis pomi*, yet the eggs of *Aphis avenae* and *Aphis sorbi* must have been included, and this of course would vitiate the results. As the writer's observations were made under similar conditions it is not necessary to present them.

*The stem mother*

The young lice which hatch from the eggs are all females and are generally referred to as *stem mothers* (Plate XVIII). The stem mothers are wingless, viviparous females reproducing without the intervention of males. The lice, when they leave the eggs, are active creatures with long legs, capable of crawling rapidly over the limbs and branches of the trees. They settle on the green tips of the opening buds (Plate VII), and, inserting their tiny beaks, begin at once to pump out the plant juices. In company with the grain aphis they may completely cover the green tips of the buds, often as many as sixty or seventy being present on a single bud. As the buds open and as more lice hatch, their numbers increase greatly, and it is not uncommon to find every bud completely covered. With the opening of the buds the lice penetrate in among the young and tender leaves and are soon almost completely hidden among the plant hairs. The lice attack also the flower buds, frequently congregating in them in such numbers as to prevent them from unfolding. They attack also the young flower stalks, which they weaken, causing the flower to fail to develop normally.

The young lice develop rapidly provided weather conditions are favorable. As they grow they shed their skins at irregular intervals, passing thru four molts before reaching maturity. A detailed description of the stages is given below. In the writer's cages the first eggs hatched on April 21 (in 1915) and the stem mothers began producing young on May 10, a period of twenty days being required in this case for them to reach maturity. As that spring was very cold the development of the insects

was retarded. In the experiments of the preceding year the stem mothers that hatched first also required twenty days to reach maturity. Lice hatching at later dates, such as from April 26 to April 30, required from twelve to fifteen days to reach maturity, the stem mothers beginning to produce young from May 10 to May 12. In general it may be said that for the year in question (1915) the stem mothers reached maturity and began producing young from May 11 to May 14. At that time the trees were coming into full bloom and conditions were ideal for the young lice to cluster on the opening flowers as well as on the tender leaves.

*Activities*

After the last molt, the stem mothers become mature and begin producing young within a very short time, in many cases within twenty-four hours after the last molt or even within a shorter period. This time, however, varies greatly, apparently being dependent on weather conditions and particularly on moisture. In these experiments reproduction was delayed for several days in some instances, and several of the stem mothers died without producing any young. In the case of stem mothers placed on caged trees in the outdoor insectary, reproduction began, when the weather was clear (tho cool), usually within twenty-four hours after the last molt. Owing to the lack of necessary equipment it has been impossible to study the relation of moisture or temperature to the activities of any stages of this insect, or the effect of these factors on the predacious or parasitic enemies. General observations have been made, but it seems unwise to include them here as no accurate experimental data are at hand.

After reaching maturity the stem mothers do not move about over their host plant to any extent except when they become overcrowded or are disturbed. Under such conditions they seek new quarters and may spread generally over the tree on which they are located.

*Reproductive capacity*

As has already been pointed out, in 1915 reproduction was just becoming general when the apple trees were coming into full bloom. Many stem mothers, thru unknown causes, began reproducing later. Why certain stem mothers should begin reproducing considerably later than others under apparently similar conditions is unknown to the writer; tentatively several causes appear operative, but none of these have been determined

experimentally. The period of reproductive activity varies considerably, as well as the total number of young produced. This is well shown in the accompanying chart (Reproduction Chart I) illustrating the productive period and the daily rate of reproduction. On examination of the chart it may be seen that for five stem mothers the reproductive period varies from 29 to 34 days, the average daily rate of production varying from 1.38 to 2.41. The total number of young produced varied from 40 to 77. The greatest number of young produced by any one individual during a period of twenty-four hours was 10, in the case of stem mother 129. The total length of life from the time of hatching until normal death occurred varied but little, being only from 47 to 55 days in the case of the five insects reared under such conditions as to produce the normal life cycle.

From an examination of the chart it may be observed that the period of reproductive activity extends from the beginning of the blossoming period almost up to the beginning of the ordinary June drop for apples.

*Description of stages*

*First instar* (Plate XVIII).— Length 0.56–0.64 mm.; width 0.28–0.30 mm.

The newly hatched nymphs are dark green, the legs and the antennae being dark yellowish green. The eyes and the cornicles are black. On the dorsal aspect of the head are two dark chitinized areas, one on each side of the median line. The antennae are 4-jointed, with sensoria present at the distal end of the third joint and at the proximal end of the flagellum of the fourth joint.

At this stage the legs and the antennae are long as compared with the size of the body, and this gives the young lice a sprawling appearance.

This stage grows very considerably before molting, becoming elongate-oval and measuring over 0.72 mm. in length.

*Second instar.*— Length 0.96–1.04 mm.; width 0.48–0.50 mm.

The nymph in this stage is yellowish green, never bright nor grass-green in color. The cornicles and the cauda are black, the legs and the distal half of the antennae dusky. There are two prominent dusky patches on the head, one on each side of the median line. The antennae are 5-jointed. The cornicles are cylindrical, slightly tapering toward their tips, 0.04 mm. in length.

## REPRODUCTION CHART I. APHIS POMI

### Reproductive capacity of stem mother, 1915

| No. | May | | | | | | | | | | | | | | | | | | | June | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | | | | | | |
| 112 | .. | 1 | 1 | 4 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 2 | 0 | 2 | 3 | 1 | 1 | 3 | 2 | 3 | 1 | 6 | 3 | 1 | 3 | 5 | 3 | 3 | 3 | 0 | 1 | .. | .. | .. | .. | 30 | 2.00 | 6 | 60 | June 19 | 55 |
| 119 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 4 | 2 | 1 | 0 | 0 | 0 | 4 | 0 | 4 | 2 | 2 | 4 | 2 | 5 | 0 | 1 | 0 | .. | .. | .. | .. | .. | 29 | 1.38 | 5 | 40 | June 10 | 47 |
| 121 | 4 | 4 | 0 | 4 | 0 | 0 | 2 | 0 | 2 | 3 | 3 | 3 | 1 | 0 | 1 | 0 | 2 | 0 | 4 | 2 | 1 | 2 | 4 | 2 | 2 | 2 | 8 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 34 | 1.79 | 8 | 61 | June 18 | 55 |
| 123 | 3 | 3 | 2 | 0 | 0 | 1 | 1 | 2 | 2 | 2 | 2 | 0 | 0 | 5 | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 3 | 3 | 1 | 3 | 2 | 2 | 2 | 4 | 2 | 0 | 1 | 0 | .. | 33 | 1.67 | 5 | 55 | June 15 | 52 |
| 129 | 4 | 0 | 5 | 2 | 1 | 0 | 1 | 0 | 7 | 1 | 3 | 4 | 0 | 2 | 4 | 0 | 0 | 2 | 4 | 3 | 3 | 2 | 4 | 10 | 2 | 5 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | .. | .. | 32 | 2.41 | 10 | 77 | June 19 | 53 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages ..... | 31.6 | 1.85 | | 58.6 | | 52.4 |

### Reproductive capacity of second generation, 1915

| No. | June | | | | | | | | | | | | | | | | | | | | | | | | | | July | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apterous females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | | | | | | | | | | | |
| 162 | .. | .. | .. | .. | .. | .. | 1 | 1 | 1 | 1 | 5 | 6 | 3 | 5 | 4 | 5 | 5 | 3 | 1 | 6 | 2 | 1 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | .. | .. | .. | .. | .. | 23 | 2.52 | 6 | 58 | July 9 | 56 |
| 163 | .. | .. | .. | .. | .. | .. | 2 | 0 | 3 | 2 | 5 | 7 | 6 | 3 | 4 | 5 | 6 | 3 | 1 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | .. | .. | .. | .. | .. | 24 | 2.38 | 7 | 57 | July 12 | 56 |
| 164 | .. | .. | .. | .. | .. | .. | .. | 1 | 4 | 3 | 4 | 3 | 5 | 2 | 4 | 7 | 2 | 3 | 4 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 18 | 2.67 | 7 | 48 | July 2 | 46 |
| 134 | .. | 2 | 5 | 5 | 4 | 6 | 3 | 0 | 3 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 13 | 2.61 | 6 | 34 | June 19 | 36 |
| 147 | .. | 2 | 3 | 3 | 6 | 0 | 2 | 0 | 0 | 1 | 1 | 7 | 4 | 2 | 2 | 3 | 1 | 0 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 16 | 2.31 | 7 | 37 | June 20 | ..... |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages ..... | 18.8 | 2.50 | | 46.8 | | 48.5 |
| | Winged females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 151 | 4 | 1 | 2 | 2 | 2 | 2 | 3 | 4 | 1 | 3 | 2 | 3 | 1 | 4 | 0 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 14 | 2.43 | 4 | 34 | June 20 | 38 |
| 155 | .. | .. | .. | .. | 1 | 8 | 2 | 1 | 3 | 1 | 0 | 2 | 1 | 8 | 5 | 2 | 1 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 13 | 2.69 | 8 | 35 | June 25 | ..... |
| 157 | .. | .. | 1 | 2 | 1 | 3 | 1 | 2 | 2 | 4 | 3 | 4 | 2 | 3 | 3 | 2 | 2 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 15 | 2.33 | 4 | 35 | June 20 | ..... |
| 159 | .. | .. | .. | .. | 1 | 5 | 2 | 2 | 2 | 1 | 5 | 7 | 4 | 4 | 3 | 3 | 1 | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 13 | 3.08 | 7 | 40 | June 20 | 38 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages ..... | 13.7 | 2.63 | | 36 | | 38 |

## REPRODUCTION CHART I. APHIS POMI (*continued*)

### Reproductive capacity of third generation, 1915

| No. | June | | | | | | | | | | | | | | | July | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apterous females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | | | | | | |
| 168 | 3 | 1 | 5 | 8 | 6 | 3 | 3 | 4 | 2 | 0 | 6 | 2 | 3 | 3 | 3 | 3 | 3 | 2 | 0 | | | | | | | | | | 18 | 3.33 | 8 | 60 | July 5 | 32 |
| 172 | | | | 2 | 9 | 6 | 2 | 4 | 1 | 1 | 1 | 4 | 3 | 0 | 4 | 3 | 0 | 1 | 0 | 1 | 1 | | | | | | | | 18 | 2.39 | 9 | 43 | July 6 | 33 |
| 174 | | | | 6 | 8 | 4 | 2 | 8 | 3 | 2 | 2 | 4 | 1 | 3 | 4 | 2 | 6 | 0 | 0 | | | | | | | | | | 14 | 3.93 | 8 | 55 | July 2 | 29 |
| 175 | | | | 3 | 7 | 5 | 1 | 4 | 4 | 1 | 2 | 2 | 1 | 6 | 2 | 6 | 3 | 5 | 4 | 5 | 3 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 24 | 2.92 | 7 | 70 | July 13 | 40 |
| | Apterous forms from winged females | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 18.5 | 3.14 | | 57 | | 33.5 |
| 177 | | | | 6 | 7 | 4 | 3 | 7 | 0 | 3 | 4 | 1 | 3 | 0 | 3 | 2 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | | | | | | 20 | 2.50 | 7 | 50 | July 16 | 43 |
| 178 | | | | 2 | 9 | 5 | 5 | 3 | 2 | 2 | 4 | 1 | 7 | 0 | 6 | 6 | 4 | 4 | 6 | 2 | 3 | 0 | 2 | 0 | | | | | 20 | 3.65 | 9 | 73 | July 17 | 44 |
| 179 | | | | 1 | 0 | 0 | 5 | 6 | 1 | 2 | 6 | 4 | 1 | 4 | 5 | 3 | 2 | 3 | 3 | 2 | 4 | 1 | 2 | 1 | 0 | | | | 21 | 2.67 | 6 | 56 | July 17 | 44 |
| 180 | | | | 4 | 5 | 8 | 3 | 6 | 1 | 0 | 5 | 1 | 6 | 2 | 3 | 2 | 4 | 4 | 2 | 0 | 0 | | | | | | | | | 16 | 3.50 | 8 | 56 | July 4 | 33 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 19.2 | 3.08 | | 58.8 | | 41 |

690

### Reproductive capacity of fourth generation, 1915

| No. | June | | | | | | | | | July | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apterous females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | | | | | |
| 182 | | | | 4 | 4 | 3 | 3 | 4 | 6 | 1 | 3 | 5 | 3 | 5 | 3 | 5 | 1 | 3 | 5 | 3 | 2 | 1 | 2 | 2 | 3 | 3 | 0 | | | 23 | 3.22 | 6 | 74 | July 20 | 38 |
| 184 | | | 4 | 3 | 2 | 2 | 4 | 3 | 8 | 3 | 3 | 6 | 9 | 6 | 3 | 6 | 2 | 4 | 4 | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | | | 24 | 3.42 | 9 | 82 | July 18 | 37 |
| 187 | 3 | 1 | 2 | 5 | 2 | 4 | 3 | 5 | 4 | 5 | 3 | 9 | 5 | 6 | 5 | 3 | 1 | 2 | 3 | 0 | 1 | 0 | | | | | | | | 21 | 3.43 | 9 | 72 | July 19 | 35 |
| 189 | 4 | 2 | 2 | 5 | 2 | 4 | 3 | 7 | 7 | 5 | 6 | 9 | 2 | 9 | 0 | 9 | 1 | 2 | 2 | 1 | 3 | 1 | 0 | 1 | 1 | 0 | | | | 25 | 3.52 | 9 | 88 | July 18 | 36 |
| 190 | | | 3 | 5 | 2 | 2 | 2 | 8 | 3 | 4 | 4 | 2 | 8 | 2 | 6 | 3 | 1 | 7 | 1 | 1 | 1 | 5 | 0 | | | | | | | 20 | 3.50 | 8 | 70 | July 14 | 30 |
| 192 | 3 | 3 | 3 | 3 | 2 | 2 | 3 | 8 | 6 | 2 | 6 | 5 | 8 | 5 | 3 | 6 | 1 | 1 | 7 | 3 | 3 | 3 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 28 | 3.25 | 8 | 91 | July 22 | 39 |
| | Apterous form from winged female | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 23.5 | 3.39 | | 79.5 | | 35.8 |
| 183 | 2 | 4 | 0 | 2 | 1 | 2 | 3 | 0 | 4 | 2 | 1 | 1 | 3 | 2 | 0 | | | | | | | | | | | | | | 14 | 1.93 | 4 | 27 | July 9 | ..... |

## REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of fifth generation, 1915

| No. | July | | | | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apterous females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | | | | | | |
| 194 | 3 | 5 | 2 | 5 | 2 | 3 | 6 | 3 | 4 | 5 | 7 | 8 | 2 | 3 | 8 | 0 | 0 | | | | | | | | 15 | 4.40 | 8 | 66 | July 21 | 27 |
| 199 | 6 | 1 | 6 | 6 | 3 | 4 | 6 | 4 | 5 | 6 | 6 | 5 | 5 | 0 | 5 | 0 | 1 | 0 | | | | | | | 17 | 4.06 | 6 | 69 | July 22 | 27 |
| 201 | 5 | 2 | 3 | 2 | 5 | 4 | 4 | 4 | 4 | 5 | 11 | 3 | 5 | 4 | 6 | 0 | 1 | 3 | 0 | 0 | | | | | 18 | 3.94 | 11 | 71 | July 26 | 32 |
| | | | | | | | | | | | | | | | | | | | | | | | | | 16.7 | 4.13 | | 68.7 | | 28.7 |
| | Averages | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Apterous forms from winged females | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 204 | | 2 | 4 | 0 | 3 | 3 | 2 | 2 | 4 | 3 | 3 | 10 | 3 | 0 | 0 | | | | | | | | | | 12 | 3.25 | 10 | 39 | July 19 | 25 |
| 207 | | 4 | 3 | 5 | 2 | 1 | 3 | 5 | 2 | 4 | 7 | 5 | 4 | 6 | 4 | 5 | 1 | 1 | 2 | 2 | 4 | 0 | 1 | 0 | 22 | 3.23 | 7 | 71 | July 29 | 34 |

Reproductive capacity of sixth generation, apterous female, 1915

| No. | July | | | | | | | | | | | | | | | | | August | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | | | | | |
| 217 | | 7 | 8 | 7 | 4 | 8 | 6 | 0 | 5 | 3 | 4 | 5 | 5 | 3 | 3 | 3 | 3 | 2 | 1 | 3 | 0 | 0 | | | | 19 | 4.21 | 8 | 80 | Aug. 6 | 33 |
| 218 | 1 | 9 | 6 | 7 | 5 | 3 | 4 | 2 | 0 | 0 | 3 | 3 | 2 | 1 | 0 | 1 | 4 | 0 | 0 | 0 | | | | | | 17 | 3.00 | 9 | 51 | Aug. 1 | 28 |
| 219 | | | 8 | 8 | 5 | 7 | 9 | 2 | 2 | 4 | 4 | 2 | 3 | 1 | 0 | 1 | 3 | 0 | 0 | | | | | | | 15 | 3.93 | 9 | 59 | Aug. 1 | 28 |
| 220 | | | | | | 5 | 0 | 2 | 9 | 1 | 4 | 5 | 5 | 5 | 4 | 5 | 3 | 8 | 4 | 5 | 0 | 1 | 0 | 1 | 0 | 19 | 3.53 | 9 | 67 | Aug. 10 | ..... |
| 221 | | 10 | 5 | 7 | 4 | 2 | 5 | 2 | 4 | 2 | 5 | 6 | 5 | 0 | 0 | | | | | | | | | | | 12 | 4.75 | 10 | 57 | July 27 | ..... |
| | | | | | | | | | | | | | | | | | | | | | | | | | | 16.4 | 3.88 | | 62.8 | | 29.7 |
| | Averages | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

## REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of seventh generation, apterous female, 1915

| No. | July | | | | | | | | August | | | | | | | |

## REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of ninth generation, apterous female, 1915

| No. | August | | | | | | | | | | | | | | | | September | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | | | | | | |
| 268 | 3 | 5 | 6 | 2 | 2 | 1 | 3 | 3 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | . | . | . | . | . | | 21 | 1.81 | 6 | 38 | Sept. 5 | 34 |
| 272 | . | 6 | 3 | 1 | 3 | 2 | 1 | 4 | 4 | 6 | 4 | 1 | 1 | 2 | 2 | 4 | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 0 | . | . | | 23 | 2.30 | 6 | 53 | Sept. 9 | 37 |
| 279 | 4 | 3 | 4 | 1 | 3 | 2 | 4 | 1 | 5 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | . | . | . | . | . | . | . | . | . | . | | 15 | 2.07 | 5 | 31 | Aug. 31 | 29 |
| 280 | 3 | 5 | 3 | 4 | 1 | 1 | 1 | 4 | 0 | 2 | 2 | 0 | 0 | 3 | 1 | 1 | 0 | 0 | . | . | . | . | . | . | . | . | . | | 16 | 1.94 | 5 | 31 | Sept. 4 | 34 |
| 282 | 4 | 2 | 3 | 3 | 3 | 2 | 2 | 3 | 4 | 4 | 4 | 3 | 4 | 2 | 1 | 9 | 3 | 1 | 0 | 7 | 2 | 0 | 4 | 5 | 2 | 0 | 0 | | 25 | 3.08 | 9 | 77 | Sept. 8 | 36 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | 20 | 2.24 | | 46 | | 34 |

Reproductive capacity of tenth generation, apterous female, 1915

| No. | August | | | | | | | | September | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | | | | | | | |
| 286 | 2 | 2 | 1 | 2 | 2 | 2 | 4 | 3 | 1 | 1 | 2 | 3 | 1 | 6 | 5 | 6 | 2 | 2 | 0 | 2 | 1 | 3 | 1 | 2 | 0 | . | . | | 24 | 2.33 | 6 | 56 | Sept. 17 | 33 |
| 288 | 2 | 4 | 1 | 2 | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 1 | 5 | 3 | 8 | 2 | 1 | 6 | 3 | 3 | 2 | 3 | 2 | 0 | 1 | 0 | 0 | | 25 | 2.24 | 8 | 56 | Sept. 20 | 36 |
| 290 | 2 | 3 | 2 | 1 | 3 | 1 | 3 | 1 | 0 | 3 | 0 | 6 | 1 | 4 | 4 | 5 | 2 | 3 | 4 | 2 | 3 | 2 | 4 | 1 | 0 | 0 | . | | 24 | 2.50 | 6 | 60 | Sept. 20 | 36 |
| 296 | . | 6 | 1 | 3 | 3 | 1 | 3 | 3 | 0 | 2 | 3 | 4 | 1 | 5 | 6 | 1 | 4 | 3 | 3 | 1 | 0 | 0 | . | . | . | . | . | | 19 | 2.79 | 6 | 53 | Sept. 15 | 31 |
| 300 | . | . | . | . | 2 | 2 | 2 | 0 | 1 | 3 | 3 | 4 | 5 | 3 | 5 | 6 | 6 | 4 | 2 | 1 | 0 | 4 | 3 | 1 | 0 | 0 | . | | 20 | 2.85 | 6 | 57 | Oct. 6 | 50 |
| 301 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | 4 | 4 | 4 | 0 | 0 | 3 | 3 | 2 | 0 | 2 | 2 | . | . | . | | 24 | 1.67 | 4 | 40 | Sept. 19 | ..... |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | 22.7 | 2.40 | | 53.7 | | 37.2 |

## REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of eleventh generation, apterous female, 1915

| No. | September | | | | | | | | | | | | | | | | | | | | | | | | | | October | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | | | | | | |
| 306 | . | . | . | 5 | 4 | 2 | 5 | 0 | 4 | 2 | 0 | 2 | 0 | 13 | 2 | 3 | 0 | 5 | 1 | 0 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 16 | 3.00 | 13 | 48 | Sept. 22 | 29 |
| 308 | . | . | 2 | 4 | 4 | 5 | 6 | 3 | 2 | 4 | 4 | 6 | 2 | 3 | 7 | 1 | 0 | 1 | 1 | 4 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 30 | 2.13 | 7 | 64 | Oct. 9 | 46 |
| 310 | . | . | . | 2 | 3 | 6 | 2 | 3 | 3 | 3 | 2 | 2 | 5 | 1 | 3 | 3 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | . | 29 | 1.79 | 6 | 52 | Oct. 8 | 45 |
| 311 | . | . | 4 | 3 | 3 | 5 | 4 | 3 | 6 | 2 | 4 | 4 | 6 | 3 | 5 | 1 | 3 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | . | . | . | 27 | 2.22 | 6 | 60 | Oct. 16 | 54 |
| 313 | 3 | 0 | 5 | 6 | 1 | 2 | 1 | 0 | 2 | 0 | 1 | 4 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 16 | 1.81 | 6 | 29 | Oct. 1 | 39 |
| 316 | . | . | . | 5 | 4 | 4 | 5 | 5 | 4 | 4 | 5 | 3 | 5 | 5 | 6 | 3 | 2 | 3 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | . | . | . | . | . | 24 | 2.92 | 6 | 70 | Oct. 1 | 38 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages ..... | 23.7 | 2.31 | | 53.8 | | 41.8 |

Reproductive capacity of twelfth generation, apterous female, 1915

| No. | September | | | | | | | | | | | | | | | | | | | | | October | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | | | | | | |
| 323 | 4 | 2 | 5 | 4 | 5 | 2 | 3 | 3 | 4 | 5 | 2 | 0 | 2 | 0 | 1 | 1 | 3 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | . | . | . | . | . | . | 27 | 2.07 | 5 | 56 | Oct. 10 | 42 |

## REPRODUCTION CHART I. APHIS POMI (*concluded*)

Reproductive capacity of thirteenth generation, apterous female, 1915

| No. | September | | | | | | | | | | | | | | | October | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | | | | | | | | | |
| 330 | 8 | 5 | 5 | 3 | 3 | 4 | 1 | 1 | 0 | 4 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 2 | 3 | 1 | 2 | 0 | 0 | 0 | 3 | 1 | 0 | 4 | 1 | 2 | 0 | 0 | *a* | | | 44 | 1.52 | 8 | 67 | Nov. 1 | 56 |
| 331 | | 6 | 4 | 7 | 4 | 5 | 1 | 0 | 2 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | | | | | | | | | 27 | 1.70 | 7 | 46 | Oct. 14 | 39 |
| 334 | 2 | 8 | 9 | 4 | 3 | 4 | 1 | 0 | 0 | 3 | 3 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 5 | 2 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | | | | | | | | | | 26 | 2.15 | 9 | 56 | Oct. 17 | 43 |
| 339 | | | 5 | 6 | 4 | 3 | 1 | 1 | 0 | 1 | 4 | 0 | 1 | 1 | 1 | 1 | 0 | 3 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | | | | | | | 27 | 1.52 | 6 | 41 | Oct. 19 | 45 |
| 340 | | 8 | 7 | 4 | 5 | 3 | 1 | 1 | 3 | 1 | 4 | 0 | 1 | 1 | 0 | 0 | 3 | 2 | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | | | | | | | | | 27 | 1.96 | 8 | 53 | Nov. 5 | 62 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages ..... | | 30.2 | 1.77 | | 52.6 | | 49 |

*a* 2 young on October 23, 25, and 29, respectively.

*Third instar.*— Length 1.28–1.30 mm.; width 0.72 mm.

In coloring and markings this instar differs but slightly from the preceding. The cauda is more prominent and the cornicles are twice as long, 0.08 mm. in length. The lateral tubercles now begin to appear on the prothoracic and abdominal segments.

*Fourth instar.*— Length 1.44–1.50 mm.; width 0.88 mm.

In this stage the nymph is yellowish green in color, with the legs, the distal half of the antennae, and the cauda dusky to black. The cornicles are dusky, with black at their tips. The dusky patches on the head are apparently absent. The antennae are 5-jointed. The cornicles now

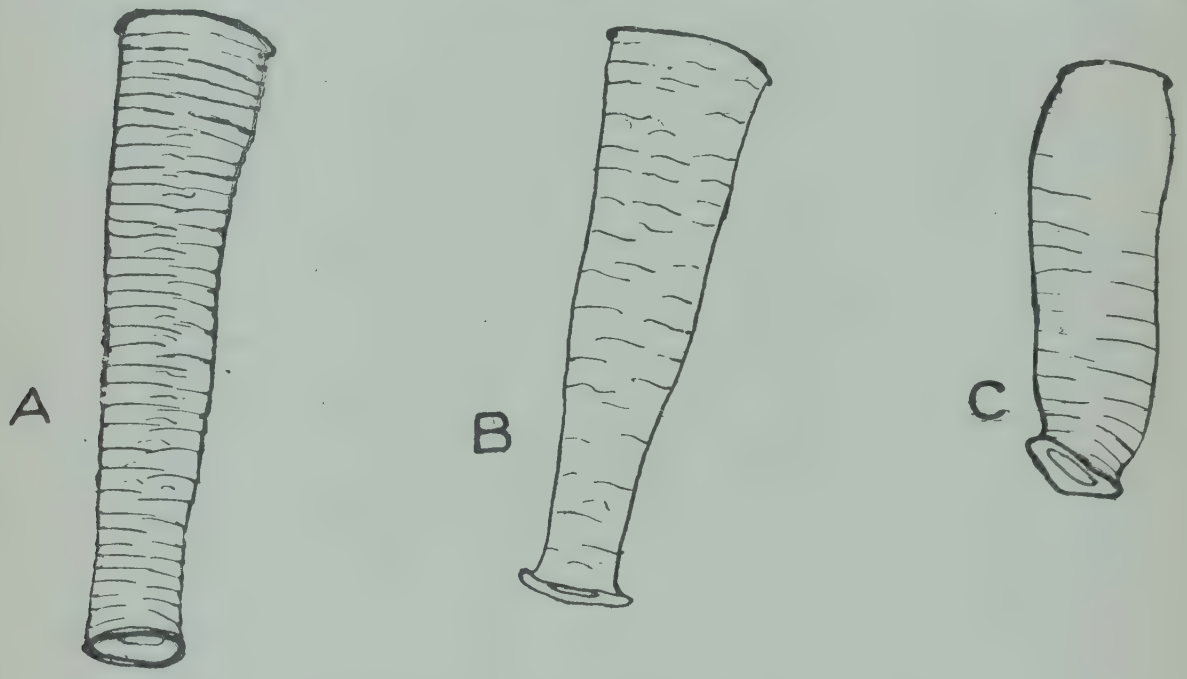



FIG. 113. CORNICLES OF MATURE STEM MOTHERS

A, *Aphis pomi*; B, *A. sorbi*; C, *A. avenae*. All drawn to same scale

measure 0.16 mm. in length. The eyes are black and are now rather prominent. The lateral tubercles on the prothoracic and abdominal segments show more distinctly than in the preceding instar, and lateral tubercles appear also on the last two thoracic segments.

*Fifth instar, mature stem mother* (Plate XIX).— Length 1.6–1.7 mm.; width 0.95–1 mm.

The head and the thorax are yellowish green, the head usually having a dusky appearance. The abdomen is bright to dark green, frequently mottled with yellowish green. The eyes are black and rather prominent. The cornicles are black, cylindrical, slightly tapering, 0.24 mm. long (fig. 113, A). The cauda is black, setose, prominent; the sub-

genital plate and the large oval area on the preceding segment are black. The antennae are 5-jointed, the third joint in some cases showing segmentation and thus giving a 6-jointed antenna. The length and number of sensoria of the antennal segments (fig. 112, A, page 685) are as follows: Segment III, 0.35 mm., sensoria 0; segment IV, 0.17 mm., sensoria 1; segment V, 0.11 + 0.15 mm., sensoria the usual group. The beak, reaching the base of the third pair of legs, is yellowish in color, with the last segment black. The legs are yellowish to dusky; the knees, the ends of the tibiae, and the tarsi are black. Lateral tubercles are present on the thorax and on the first eight abdominal segments.

*The second generation*

The young produced by the stem mothers all develop into either winged or wingless females. From close observation covering two years the writer found that over 75 per cent of this generation acquire wings and rapidly distribute the species from tree to tree and from orchard to orchard. In 1915 the first individuals of this generation began maturing the last two or three days in May and the first days of June. In the rearing cages winged forms began appearing on May 31. Under the conditions of that year, which were decidedly unfavorable, the early individuals required more than nineteen days to reach maturity, while in some of the cages twenty-five days were required.

It seems rather remarkable that so many individuals of this generation are provided with wings. Various theories have been advanced to explain the production of winged forms. The one oftenest quoted is that the condition is due to crowding, resulting in the lack of food. In cage after cage in these experiments there was neither crowding nor lack of suitable food, and yet the proportion of insects that acquired wings seemed, and actually was, as large as where there was undoubted crowding. It would seem that the production of such a high proportion of winged forms in this generation is entirely a provision by the species for its rapid and widespread distribution. It is self-evident that such a provision is eminently wise, and to account for it on a basis of crowding or lack of food appears, to say the least, highly inadequate.

*Activities*

*Wingless forms.*— The wingless forms exhibit no activities differing greatly from those of the stem mothers. After reaching maturity they

migrate until a satisfactory location is found, usually on the underside of a leaf or on the succulent new growth. Here they may congregate in considerable numbers, insert their beaks into the leaves, and, as they feed, bring forth their young. Once located they seldom move except when disturbed or when crowding becomes excessive, when they may be observed searching out new feeding places.

*Winged forms.*— The activities of the winged forms are much more varied and are of considerable significance for the species. The insects appear very excitable, and when disturbed they move about actively or readily take to flight. They do not settle permanently in any one place, but feed for shorter or longer periods on either the leaves or the succulent young growths. They deposit their young from time to time, and the species is distributed very rapidly during the early days of June. Frequently, if the stem mothers have been fairly abundant, considerable flights of the winged forms may be observed in the early days of June; and it is not at all uncommon at that time to find practically all the lower and outer leaves of trees that had previously been free of lice with two or three winged lice on each leaf.

*Reproductive capacity*

*Wingless forms.*— In the writer's rearing work, the reproductive capacity of the wingless forms was not so great as that of the stem mothers. This may be seen by consulting the chart, the reproductive capacity of five individuals varying from 34 to 58. The period of reproduction is considerably shorter than that of the stem mothers, and the daily rate of production is much higher.

*Winged forms.*— In the winged forms the number of young produced averages less than in the wingless forms, the productive period is shorter, and the average daily rate is about the same. In the case of the winged forms it was rather difficult to obtain accurate results, owing to the wandering habits of the insects and the fact that the cages, tho of considerable size, did not seem to allow normal development. From such considerations the writer is inclined to believe that the reproductive capacity shown in the experiments is too low.

*Both forms.*— From all the cage records, the total length of life of the apterous forms of this generation appears to be about the same as that of the stem mothers, whereas the winged forms have a considerably shorter life. Field observations have confirmed the cage experiments in this regard.

In comparing the reproductive capacity of this generation with that of the stem mothers, it will be observed that the period of reproductive activity is shorter, the average daily number of young produced is greater, and the total number of young is less. The total length of life is considerably shorter.

*Description of stages*

No attempt is made in this or in the following generations to describe the nymphal stages. Only the mature forms of each generation are described.

*Apterous female, second generation.*— In color markings, form, and size, this insect does not differ in any material respect from the apterous female of the third generation, which is described in detail on page 708.

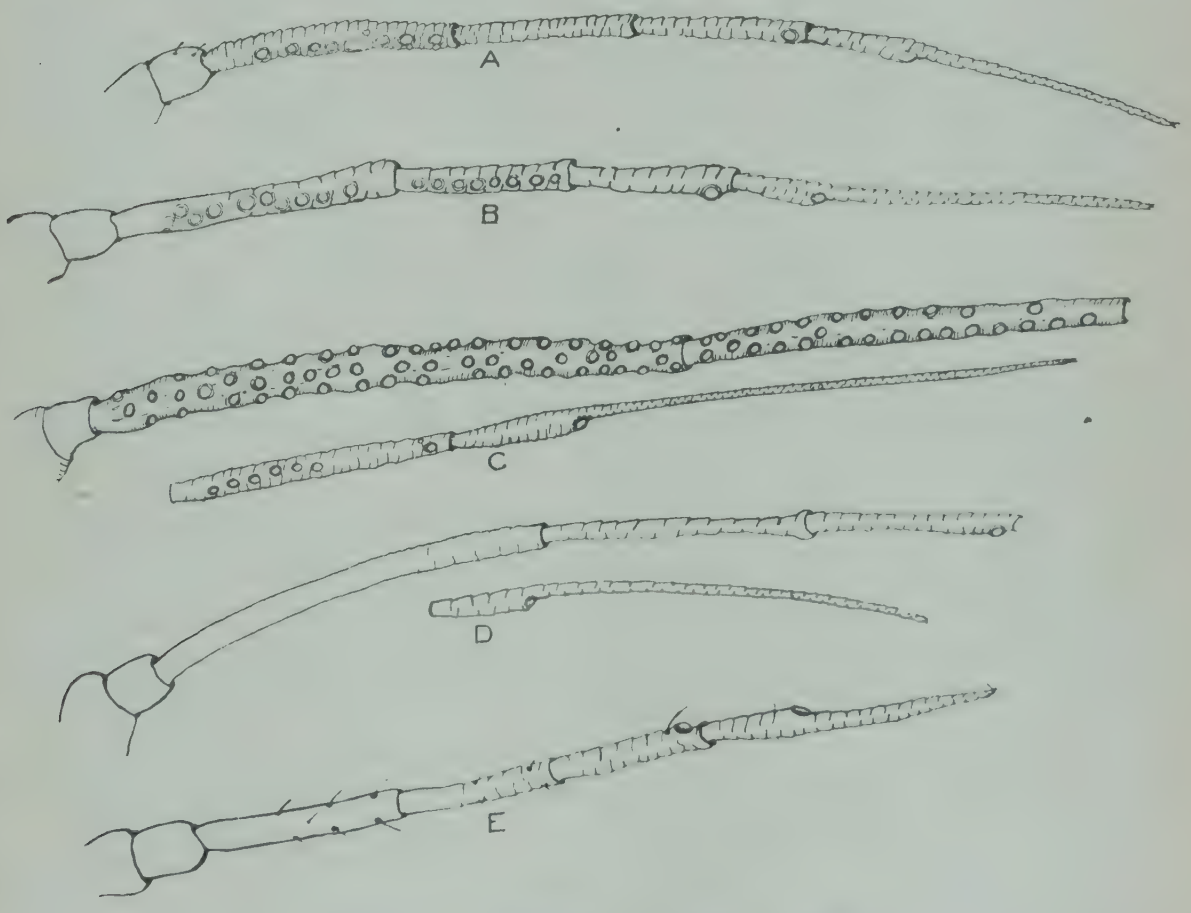



FIG. 114. ANTENNAE OF VARIOUS FORMS

A, *Aphis pomi*, winged viviparous female; B, *A. avenae*, spring migrant; C, *A. sorbi*, spring migrant; D, *A. sorbi*, apterous female on plantain; E, *A. pomi*, apterous female, summer form

*Winged viviparous female, second generation.*— Length 1.6–1.8 mm.; width 0.72–0.80 mm.; cornicles 0.28–0.32 mm. long. (The cornicles vary somewhat in length, but the majority are 0.32 mm. long.)

The abdomen is green, occasionally tinged with yellow, with three or four dusky patches on each side in front of the cornicles; the head, the thorax above and below, the cornicles, the cauda, the genital plates, the tarsi, and the distal ends of the tibiae and the femora, are black or blackish; the prothorax is margined in front and behind with green; dusky to black dorsal median patches on the sixth, seventh, and eighth abdominal segments are usually present. Lateral tubercles are present on the prothorax and on most of the abdominal segments. The eyes are a very dark red, usually appearing black, with a small posterior tubercle and with three ocelli appearing as yellow-tipped elevations. The antennae are 6-jointed; the basal two and the last two segments are dusky to blackish, the others yellowish (fig. 114, A). The cornicles are cylindrical, gradually tapering toward the distal end, with a small, well-defined flange (fig. 115, A).

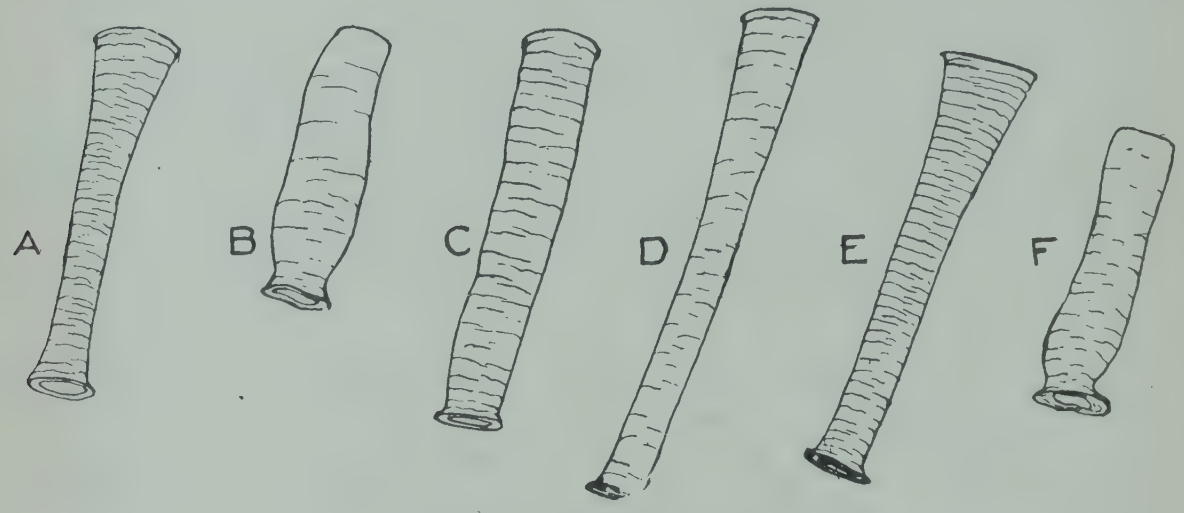



FIG. 115. CORNICLES OF VARIOUS FORMS

A, *Aphis pomi*, winged female, second generation; B, *A. avenae*, spring migrant; C, *A. sorbi*, spring migrant; D, *A. sorbi*, apterous female on plantain; E, *A. sorbi*, fall migrant; F, *A. avenae*, fall migrant. All drawn to same scale

*The third generation*

As is well known, all the summer generations of this plant louse consist of viviparous females, reproducing without the intervention of males.

In the case of the second generation, a majority, over 75 per cent, were found by the writer to be winged females. In the third generation the majority are wingless, less than 50 per cent possessing wings. This number, however, greatly aids in the rapid dispersal of the species, and this dispersal becomes very marked during the first half of June. The winged forms from the stem mothers reach their maximum numbers at that time, and are followed closely by the winged forms descended from the second generation.

In the outdoor cages the second generation began producing young on the last day or two of May and the third generation began maturing on June 12. On June 13 the wingless females of the third generation began producing young. Production of young by this generation became general about June 20.

*Activities*

The activities and habits of this generation do not differ in any marked degree from those of the preceding. However, the damage they do is more consequential. The third generation and its young congregate not only on the leaves, causing them to curl considerably, but also on the rapidly growing shoots, the fruit stems, and the fruits themselves. Usually the insects are found in company with the rosy aphis, so that from general observations one cannot state how much of the leaf curling is due to the one or to the other species. In general it may be stated that the green apple aphis (*Aphis pomi*) does not cause the leaves to curl so badly, but is a worse pest of the tender shoots (Plate VII), causing them to die in many cases and stunting them in others. It also dwarfs the young apples, making them knotty and gnarled and preventing much of the ordinary June drop — resulting in cluster fruits, so common to the orchardist. In this last type of injury, however, the rosy aphis is the worst offender, tho the green apple aphis when abundant is a serious factor in this work.

*Reproductive capacity*

Unfortunately, thru a mistake in the writer's cage work, the reproductive capacity of only the wingless forms was determined. However, there is shown in the table (Reproduction Chart I) the reproduction of wingless descendants of winged forms of the second generation and of descendants

of the wingless forms. The descendants of winged forms are indicated separately in the reproduction chart.

On consulting the table it may be seen that the average productive period is nearly identical with that of the wingless forms of the second generation. The daily production of young is much higher, on the average, and the total production is almost equal to that of the stem mothers. The length of life, however, is considerably shorter, more nearly approaching that of the winged forms of the second generation.

*Description of stages*

*Adult apterous female, third generation.*— Length 1.7–2 mm.; width 1 mm.; cornicles 0.4 mm. long.

The general shape is pyriform. The color is light green to bright yellowish green; the head is yellowish, often shading to dusky yellow. The eyes are dark red, appearing almost black. The antennae are yellowish, with the distal half dusky. The distal ends of the femora, the tibiae, and the tarsi are black. The cornicles are cylindrical, black, gradually tapering, with a distinct flange at the distal end. The cauda and the genital plate are black. Lateral tubercles are present on the prothorax and on the abdominal segments.

*Adult winged female, third generation* (Plate XXII).—The winged female of the third generation does not differ in any respect from that of the second generation and requires no separate description.

*The fourth generation*

At Ithaca the first individuals of the fourth generation reached maturity and began producing young on June 21. The production of young by this generation became more or less general about the last of June. The habits and activities of this and succeeding generations do not differ from those of the third generation and need not be discussed in any further detail.

The reproductive capacity of the fourth generation presents some interesting features. The period of reproduction is longer than that of either the second or the third generation, and the daily number produced by each individual is considerably greater. The total average production is much higher than for any preceding generation.

*Succeeding generations*

The generations of *Aphis pomi* follow one another with great regularity and rapidity. This succession may be easily grasped by examining the chart (Reproduction Chart I) and figure 116. Each generation after the first of June matured in from eight to twelve days, the maximum period being, for the eighth generation, during the last of July, and the tenth generation, in the latter half of August.

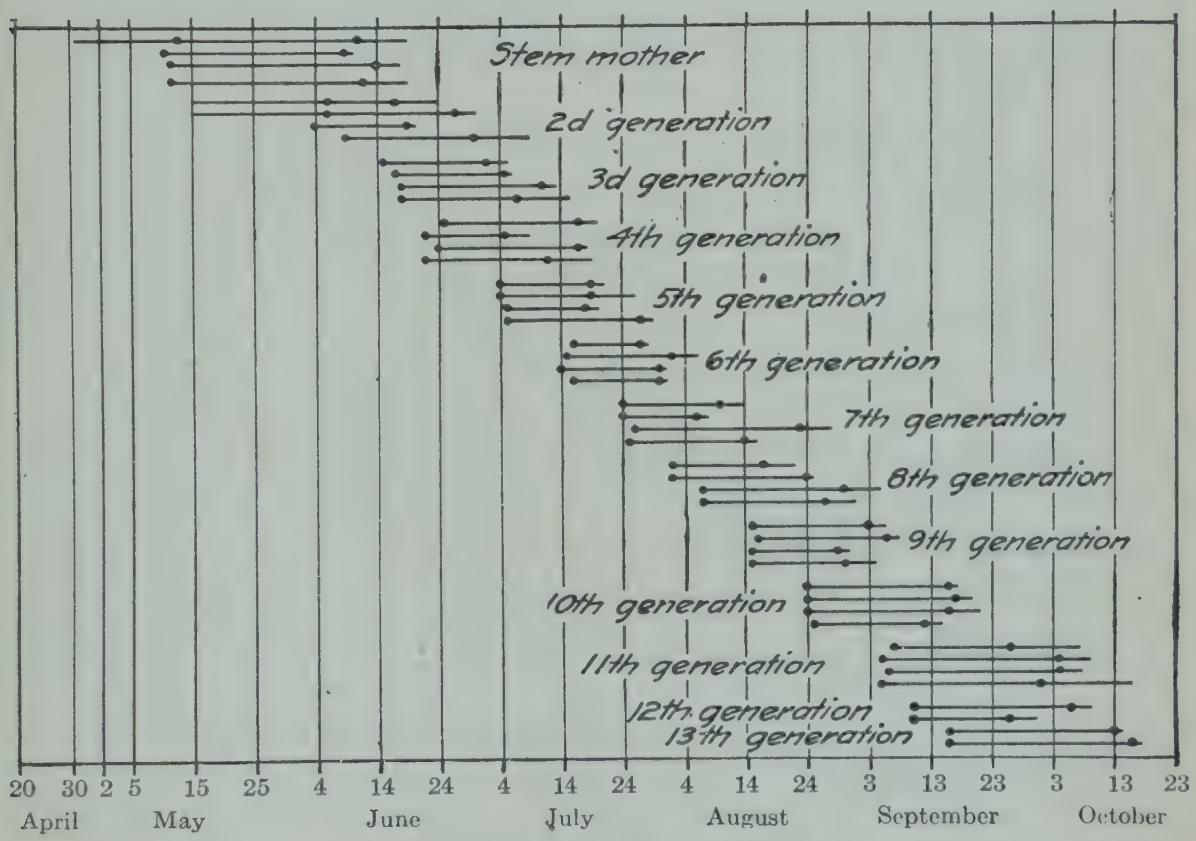



FIG. 116. GENERATIONS OF APHIS POMI

The part of the line between the round dots represents the productive period; the remainder of the line represents the period of life after production ceased

The habits and activities of these later generations present no great variations from those already discussed. Altho reproduction continues at a very high rate and there are many overlapping generations, yet the activities of the many predacious and parasitic enemies of the insects usually hold them fairly well in check. However, severe outbreaks have occurred and may be expected to continue to occur at any period during the summer. The detailed report and discussion of the parasitic and

predacious enemies of apple plant lice are deferred until a future time, in order to bring together more data and present them in a thoroly digested form.

*Number of generations*

During the season of 1915 there developed in the outdoor breeding cages fourteen viviparous generations. The fifteenth generation consisted of true males and females. This generation reached maturity about October 1. Mating began on that date and the first egg deposition was observed on October 4. Egg deposition began in the neighboring orchards at the same time.

Altho in the rearing-cage work the generation maturing on October 1 proved to consist of true males and females, yet for more than a month after that time viviparous females were producing young in the field under exactly similar conditions to those in the rearing cages. This would indicate that generations starting from young deposited by the stem mothers during the early part of June (as shown in the chart) do not begin producing the male-and-female generation until later in the fall. However, as to the average number of generations in a single season, no definite figure can be given without rearing thru a very large series, starting with the earliest- and latest-maturing stem mothers. This would involve too much detailed labor without adding materially to the knowledge of the subject. Judging from rearing work and field observations, the writer is led to conclude that in all probability there are ten full generations or more in a single season. When one considers the great reproductive capacity of each of these generations, it is not to be wondered at that severe infestations may occur at any time provided the natural checks are interfered with in any way.

*Reproductive capacity of Aphis pomi*

In consulting the reproductive capacity chart, some interesting facts may be observed. The maximum productive period (31.6 days) is for the stem mothers, and the thirteenth generation follows closely with 30.2 days. Unfortunately, no data were obtained on the fourteenth generation, owing to the death of the viviparous mothers in the special rearing cages. The minimum productive period (13.7 days) occurred only with the winged females of the second generation. The productive period varied

considerably for the other generations, tho in general it became shorter during the warmer part of the summer.

The fourth generation produced the maximum average number of young (79.5), tho not at the maximum average daily production. The minimum average number of young (36) was produced by the winged females of the second generation. The average daily production is very interesting. It gradually increased from 1.85 in the case of stem mothers to 4.13 for the fifth generation, and then gradually declined to 1.77 for the thirteenth generation.

*The male-and-female-producing generation*

In the rearing cages the fourteenth generation proved to be the male-and-female-producing generation. In their habits and activities the apterous viviparous females of this generation do not differ in any marked degree from the ordinary summer generations. They are sluggish, not showing any wandering propensities but depositing their young with quiet regularity. Owing to a series of accidents no complete records of the reproductive capacity of this generation were obtained. This is unfortunate, for such information would be highly instructive.

*Description of mature apterous female, fourteenth generation*

Length 1.92–2 mm.; width 1.04–1.2 mm.; cornicles 0.4 mm. long.

The abdomen is dark green, with yellowish brown lines often forming a somewhat reticulate pattern on the dorsal surface; the head and the thorax are yellowish brown; the distal ends of the femora, the tibiae, and the antennae, and the tarsi, the cauda, and the cornicles, are black. The cornicles are cylindrical, and are tapering and slightly flanged at their tips.

*The oviparous females and the males*

The oviparous females and the males of *Aphis pomi* are very easily distinguished from individuals of the viviparous generations. They are wingless, are much smaller than the other generations, differ considerably in their general color, and show marked differences in their habits.

In 1915 the oviparous females first reached maturity on October 1 and egg deposition began on October 4 in the rearing cages. In 1914 egg laying was first observed on October 6; in the field eggs were first observed a few days later. The egg-laying forms are active and do not

remain permanently in any one place. They may feed for a short time and then move about, locating a new place to obtain food or migrating to the twigs and depositing eggs. After each egg deposition the female returns to feed, and several days are usually occupied in the important process of egg laying. During all this time the few males that may be present actively mate with the females. In general, however, it may be said that only a small number of the females ever become fertilized, owing to the small number of males. Whether such non-fertilized eggs ever hatch has not been determined for this species, so far as is known.

As to the number of eggs that a single female is capable of laying, no definite statements can be found in literature, each author contenting himself with the barren remark that a few are laid. In the fall of 1914 a large number of experiments were conducted under normal outdoor conditions to determine this point. At the same time many dissections were made to confirm or deny the conclusions drawn from such experiments.

The table on the following page shows in a graphic form the principal data obtained.

From the table it is seen that the number of eggs laid varies considerably. Altho many females were experimented with, only a few seemed to act in a perfectly natural manner. Furthermore, it was difficult to obtain nearly mature females that had not deposited eggs, and then find a sufficient number of males, without more extensive rearings than could be made under the prevailing conditions. It would appear, from the experimenting done, that in order to secure perfectly natural conditions it is necessary to include a male in each rearing cage.

The egg-laying period extends over a considerable time. In 1914 the first eggs were deposited on October 6 and deposition continued to as late as December 1. The maximum egg deposition was reached about the latter part of October, yet many eggs were laid late in November. On November 17, 1914, a severe frost apparently froze all the females in the rearing cages. But when some of these were brought into the laboratory they revived and became active; while many of those left out of doors gradually revived, and active females were found as late as December 1. In 1915 egg deposition began on October 4, reached its maximum the latter part of the month, and continued intermittently until the end of November.

| Experiment no. | Number of lice | Date when experiment was started | Number of eggs laid | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Total number of eggs laid |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | October | | | | | | | | | | | | | | | | | | November | | | | | | | | | | | | | | | | |
| | | | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | | | | | |
| 1 | 1 ♀ | Oct. 16 | | 1 | | | 1 | | | | | ♀ dead | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| 2 | 1 ♀ | Oct. 16 | | | 1 | ♀ missing | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 3 | 1 ♀ | Oct. 16 | | 1 | | | | | | | | ♀ dead (quietly feeding up to day of its death) | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 4 | 4 ♀ | Oct. 16 | | 5 | | | 4 | 4 | | | | ♀ all dead | | | | | | | | | | | | | | | | | | | | | | | | | 13 |
| 6 | 1 ♀ | Oct. 16 | | 1 | | | 2 | 1 | | | | ♀ dead | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| 7 | 1 ♂, 1 ♀ | Oct. 21 | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | | | | ♀ dead | | | | | | 2 |
| 8 | 1 ♂, 1 ♀ | Oct. 21 | | | | | | | | | | 1 | | | | | | | 2 | | | | ♀ dead | | | | | | | | | | | | | | 3 |
| 9 | 1 ♂, 1 ♀ | Oct. 21 | | | | | | | | | | 2 | | | | | | | 1 | ♀ nearly dead | | | ♀ dead | | | | | | | | | | | | | | 3 |
| 10 | 1 ♂, 1 ♀ | Oct. 21 | | | | | | | | | | | | | | | | | 1 | | | | 2 | | | | | | | | 2 | ♀ missing | | | | | 5 |

The males are very few in number, comprising scarcely one per cent of the sexual generation. In many of the rearing cages, scarcely more than two or three males could be found among at least four to five hundred individuals. The few males present are always active, running about with great agility and mating with the females indiscriminately. Because of the very small number of males, undoubtedly hundreds and thousands of females are never fertilized.

*The oviparous female* (Plate XXIII)

Length 1.48–1.6 mm.; width 0.88 mm.; cornicles 0.32 mm. long.

The oviparous females are wingless and are regularly oval in outline. They are variable in color, but are usually yellowish green tho dark green specimens are not uncommon and very frequently practically all the green

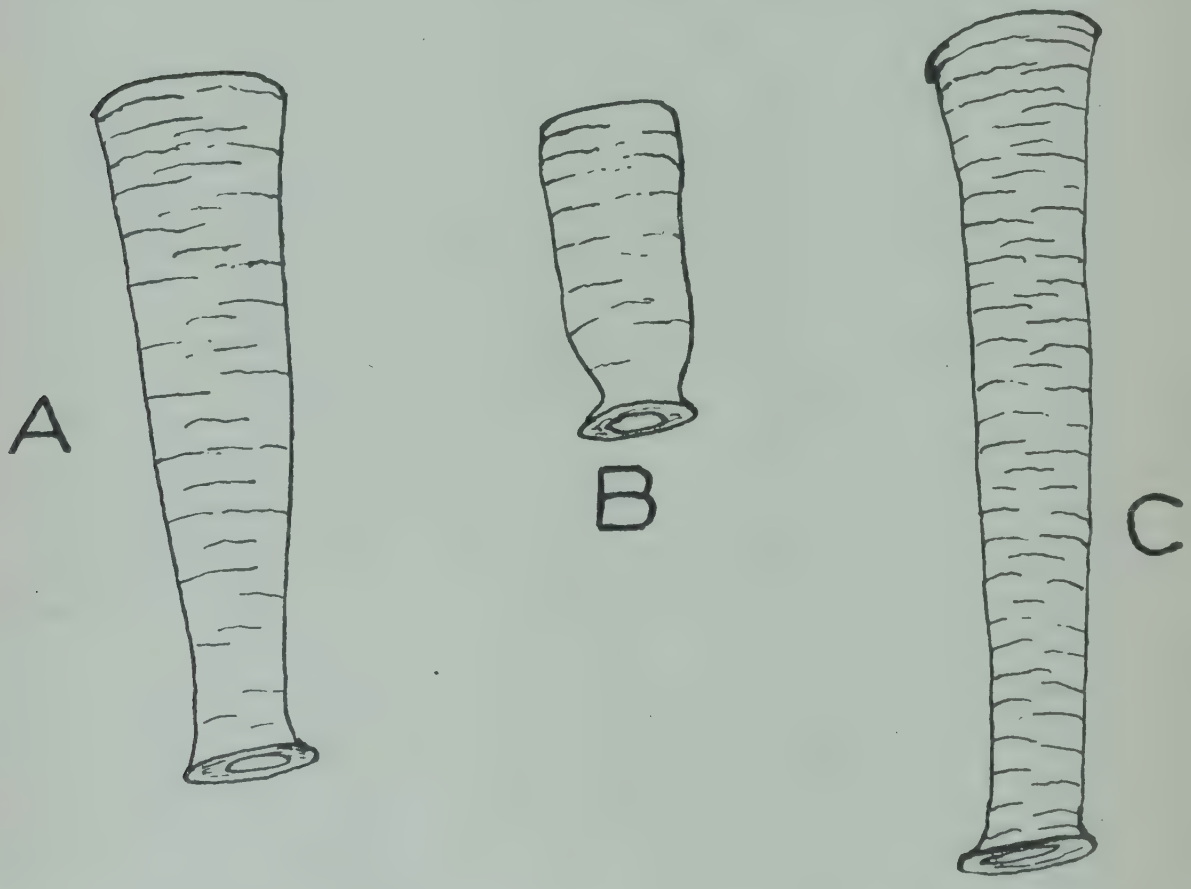



FIG. 117. CORNICLES OF VARIOUS FORMS

A, *Aphis pomi*, oviparous female; B, *A. avenae*, oviparous female; C, *A. sorbi*, oviparous female. All drawn to same scale

is lacking and the lice are from bright rusty yellow to yellow in color. Dark spots scattered over the dorsum of the abdomen are not uncommon. The head is dusky brown to yellowish; the distal half of the antenna is dusky to black, the proximal part is yellow; the legs are yellowish, with the distal ends of the femora, the tibiae, and the tarsi black; the cornicles (fig. 117, A) are black, cylindrical, gradually tapering toward their distal

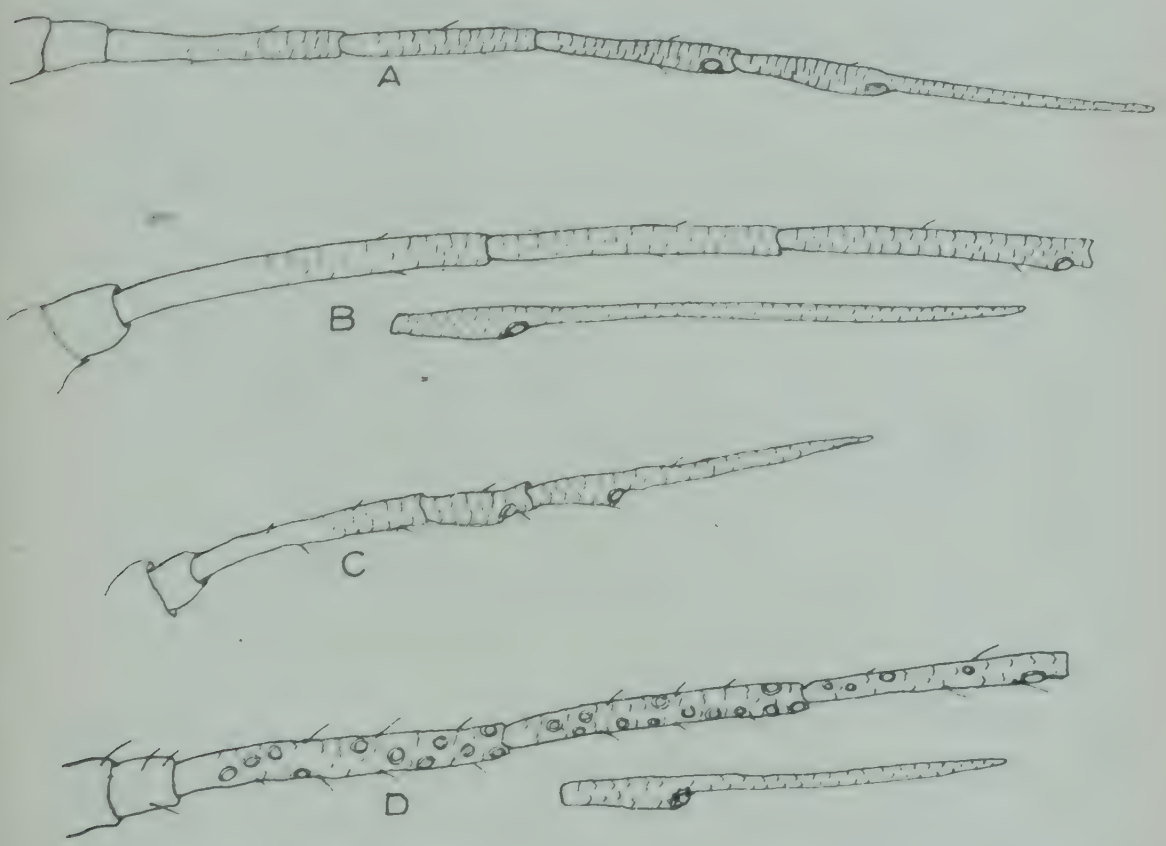



FIG. 118. ANTENNAE OF VARIOUS FORMS

A, *Aphis pomi*, oviparous female; B, *A. sorbi*, oviparous female; C, *A. avenae*, oviparous female; D, *A. pomi*, male. All drawn to same scale

ends, which are slightly flanged; the cauda is prominent and black; the segment directly in front of the subgenital plate is marked with two prominent oval black spots, one on each side of the median line. The length and number of sensoria of the antennal segments (fig. 118, A) are as follows: Segment III, 0.22 mm., sensoria 0; Segment IV, 0.15 mm. sensoria 0; Segment V, 0.16 mm., sensoria 1; Segment VI, 0.8+0.23 mm., sensoria the usual group.

The oviparous female is particularly distinguished from the females of the other generations by the position of the sensoria on the antennae and their presence on the hind tibiae. These are shown in figures 118, A, and 119, A.

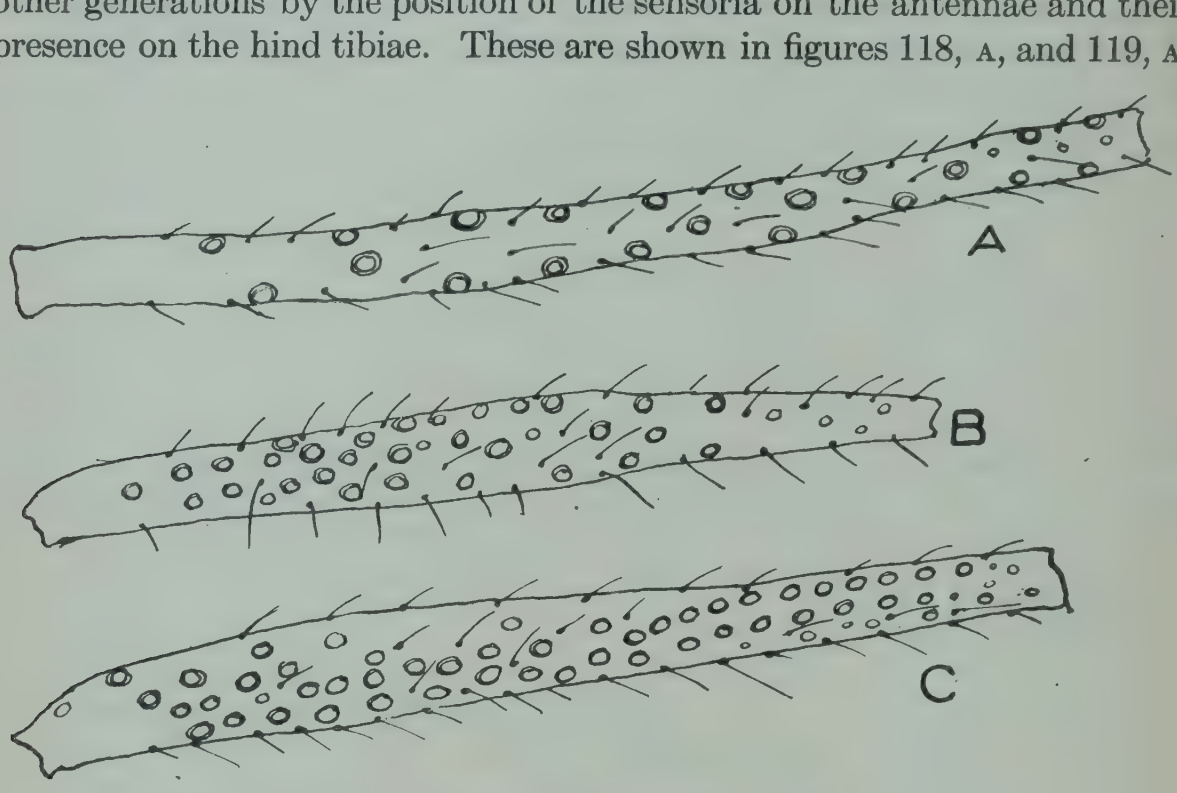



FIG. 119. HIND TIBIAE OF OVIPAROUS FEMALES
A, *Aphis pomi*; B, *A. avenae*; C, *A. sorbi*. All drawn to same scale

*The male* (Plate XXIII)

Length 0.96–1.2 mm.; width 0.48–0.56 mm.; cornicles 0.16 mm. long.

The males are wingless. The general color is brownish yellow; the head and the antennae are dusky to black; the cornicles, the cauda, and the genitalia are black; the distal ends of the femora, the tibiae, and the tarsi are dusky to black. The cornicles are cylindrical, slightly tapering toward their distal ends, with a slight flange-like expansion at their tips. The antennae are 6-jointed, nearly equaling the length of the body. The sensoria are as shown in figure 118 D. The length of the antennal segments and the number of sensoria of each are as follows: Segment III, 0.23 mm., sensoria 8–12; Segment IV, 0.22 mm., sensoria 8–11; Segment V, 0.2 mm., sensoria 3; Segment VI, 0.09+0.24 mm., sensoria the usual group.

*The egg*

The egg is oval in form, slightly flattened on the side next the bark. The length is from 0.48 to 0.56 mm. When first laid it is bright yellow

in color, and is covered with a glutinous substance which hardens with age. The color gradually changes to greenish yellow and finally to a shining jet-black. The time required for this change in color varies under normal outdoor conditions from about nine days to more than two weeks.

*The production of winged forms*

In the case of *Aphis pomi* the production of winged forms is for one purpose only; this is distribution, not migration to different host plants. For this purpose it is essential that the early generations should provide a very high proportion of winged forms, so that advantage can be taken of the large numbers and widespread occurrence of the host plant (apple). This is exactly what takes place in nature, over 75 per cent of the second generation and between 25 and 50 per cent of the third generation acquiring wings. Such a large proportion of winged forms so early in the season insures a widespread distribution and does not call for any marked production of winged forms thruout the summer; and such a condition appears to be the normal one for this species. Smith (1900 a) states that no winged forms are produced after the third generation. Sanderson (1902) and Gillette (1908) report winged forms occasionally appearing as late as the last of August. In the rearing-cage work practically every generation produced a few winged forms. In the fourth generation very few winged forms appeared, but fully 50 per cent of the fifth generation were winged. In all other generations except the ninth, the thirteenth, and the fourteenth, a few winged forms appeared. In the field winged forms were not uncommonly found during July and August, while in 1915 in the cages the last winged forms appeared on September 6. This would seem to indicate that practically all the generations during any season do and can produce winged forms. Whether the direct descendants of the winged forms may also be winged has not been positively determined for all generations. In all cases studied so far, the first generation from winged ancestry are always wingless, whereas the second generation may be either winged or wingless. Should this prove true for all winged individuals, the results would agree with those found by Professor Slingerland in his extensive studies of *Aphis avenae*.[3]

[3] Manuscript notes by Professor Slingerland.

Many opinions have been offered by various workers on the causes or factors that influence the production of winged forms in aphids. So far all these offerings are mere opinions, one of the most favored being the crowding of the insects on the food plant and the consequent reduction of the food supply. In all the writer's work of rearing thousands of individuals, crowding was eliminated and yet the percentage of winged forms for any one generation did not seem to vary. The question of the production of winged forms in aphids is one deserving deeper study than has yet been devoted to it, and the results might prove of great economic importance.

### *Food plants*

The green apple aphis is very restricted in its host plants, being confined to a few very closely related forms. The author has found the species on the following food plants: apple (*Pyrus malus* L.), pear (*Pyrus communis* L.), American crab (*Pyrus coronaria* L.), mountain ash (*Pyrus americana* Marsh and *P. aucuparia* L.), hawthorn (*Crataegus oxyacantha* L. and other species of Crataegus), and quince (*Cydonia* spp.).

Of these food plants the apple is the one most generally attacked and injured. Some varieties of apples are more susceptible than others, and from the writer's observations the following appear to be the most susceptible to injury: Twenty Ounce, Maiden Blush, King, Fall Pippin, Greening, and Baldwin.

## THE ROSY APPLE APHIS

## (*Aphis sorbi* Kaltenbach)

Altho the species *Aphis sorbi* was recognized at an early date (1854) by Fitch under the name *Aphis malifoliae*, yet, like *Aphis pomi* and *Aphis avenae*, it has been and still is greatly confused in the literature. Its characteristic work on the apple, and its bionomics, are very different from those of either of the other two species named, and had a serious study been made of its life economy all this confusion would have been avoided. Recently two rather extensive papers on the species have been published, so that its work, life history, and distribution are now becoming well known. The present paper is based on extensive rearing experiments made at Ithaca during the seasons of 1914, 1915, and 1916, and the manuscript was practically completed before the publication of the reports of Brittain (1915 b) and Baker and Turner (1916 b).

SYNONYMY

The synonymy of *Aphis sorbi* is in a rather chaotic condition. Since Sanderson's work in 1901 and 1902, the species has been generally known as *Aphis sorbi* Kaltenbach, altho a few workers have doubted the correctness of this view. Recently Baker and Turner (1916 b), after an examination of European specimens of *Aphis sorbi* taken on *Sorbus* spp. in the same region as the original material, concluded that the American species is distinct and should be known as *Aphis malifoliae* Fitch. Their conclusions do not seem to the writer to be well founded. They admit the almost exact identity of the European and American specimens, both in color markings and in morphological characters. The only characters they use in making their separation in the wingless forms are the relative lengths of the cornicles and antennal segments, and the size of the lateral tubercles. In the winged forms the only characters used are the relative lengths of the antennal segments. In support of these views Baker and Turner give two tables of measurements, one of four individuals and the other of six, taken at random. These tables show a relatively small, tho apparently definite, variation in length. However, on consulting the body of the work the variation in the lengths of these same characters is found to be much greater and to overlap very considerably for the two species. Before these characters can be given weight, it should be shown that in a long series of measurements the means for *Aphis sorbi* Kalt. and *Aphis malifoliae* Fitch are distinct and do not completely overlap. Furthermore, the lengths of antennal segments and cornicles in aphids have, to say the least, been shown to be poor morphological characters on which to base specific determinations, unless coupled with other marked differences.

From a careful reading of the literature and from the considerations just mentioned, the author is not prepared to accept the conclusions of Baker and Turner.

Recently Theobald (1916) also has attempted to untangle the synonymy of this species, and he concludes that it should be known as *Aphis kochii* Schouteden. *Aphis kochii* was the name given by Schouteden (1903) to *Aphis pyri* Koch, as the name *pyri* had already been preoccupied by Boyer de Fonscolombe (1841). Koch's (1854–57) description of this species does not agree with the species *Aphis sorbi* Kalt., and the writer is convinced that the latter should stand as a distinct species, for the

present at least. However, Theobald's description undoubtedly refers to *Aphis sorbi* Kalt., not *Aphis kochii* Schouteden (*Aphis pyri* Koch).

The following table presents what the writer considers the synonymy of this species:

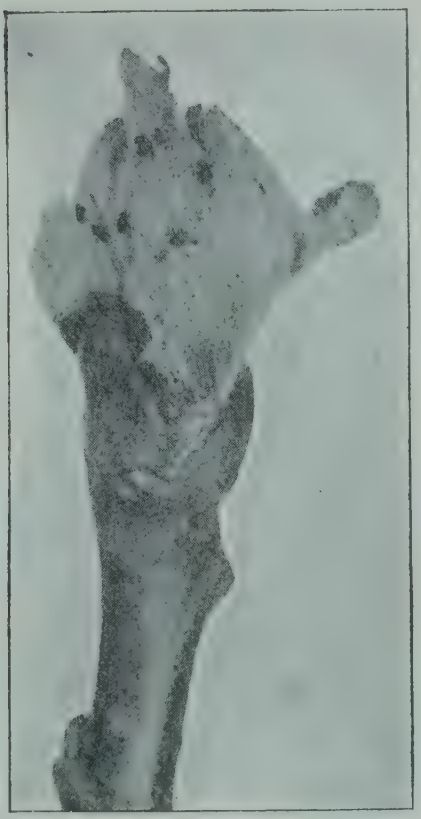
**Aphis sorbi** Kaltenbach
*Aphis pyri* Boyer of Koch, not *Aphis pyri* Boyer
*Aphis malifoliae* Fitch
*Aphis kochii* Schouteden of Theobald, not *Aphis kochii* Schouteden
*Aphis pyri* Boyer of Gillette and Taylor, not *Aphis pyri* Boyer

## HISTORICAL

The rosy apple aphis is a European species which was introduced into America at an early date; when or where this introduction took place cannot be determined because of the confusion in literature of the three species now known to be common on apple. Very little is known of the history of this species in America, and because of the meagerness of references and descriptions it seems impossible to do more than summarize the situation.

Fitch (1855 a) first described what is undoubtedly the winged fall migrant of this species under the name *Aphis malifoliae*. The material on which his description was based was collected on apple leaves in Mercer County, Illinois, on October 4, 1854. Thomas (1879) considers Fitch's species as valid, and presents a description copied largely from the original. However, he adds his own observations and concludes that this species is as common and widespread in southern Illinois as is *Aphis mali* Fabr. (this includes *Aphis pomi* De G. and *Aphis avenae* Fabr.). The next positive reference to this species is by Comstock (1894). His reference to *Aphis sorbi* is given with a question mark. However, thru the kindness of J. J. Davis, who has recently examined the Monell collection, the writer can state that the species to which Comstock referred is *Aphis sorbi* Kalt. Mr. Davis found specimens of this species sent by M. V. Slingerland in September, 1893, to Monell, and Comstock's reference is certainly to this material.

Lugger (1900) refers to this species and presents figures illustrating the insect and its work, but does not state that he found it in Minnesota. The first real work on the bionomics of this species was by Sanderson (1901 and 1902). Since that time various short articles have appeared in widely separated parts of the United States, the only detailed accounts

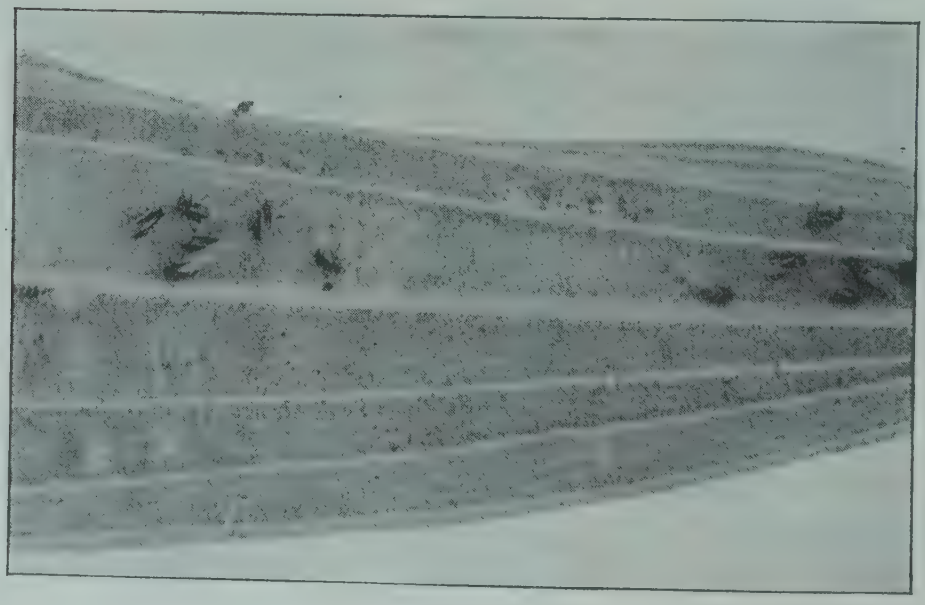


YOUNG STEM MOTHERS ON AN OPENING BUD. MAGNIFIED

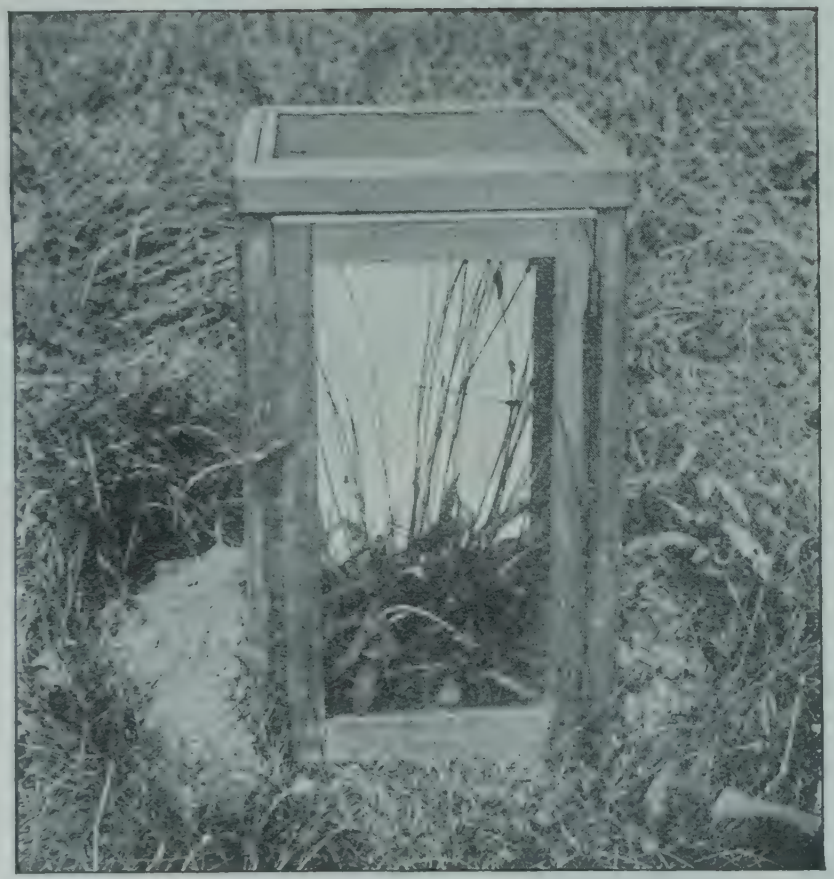
EGGS OF APHIS POMI, A. SORBI, AND A. AVENAE. MAGNIFIED

APHIS POMI CLUSTERED ON A TENDER APPLE SHOOT

CAGE ENCLOSED WITH CHEESECLOTH, IN WHICH ARE GROWING A SEEDLING APPLE AND NARROW- AND BROAD-LEAVED PLANTAINS

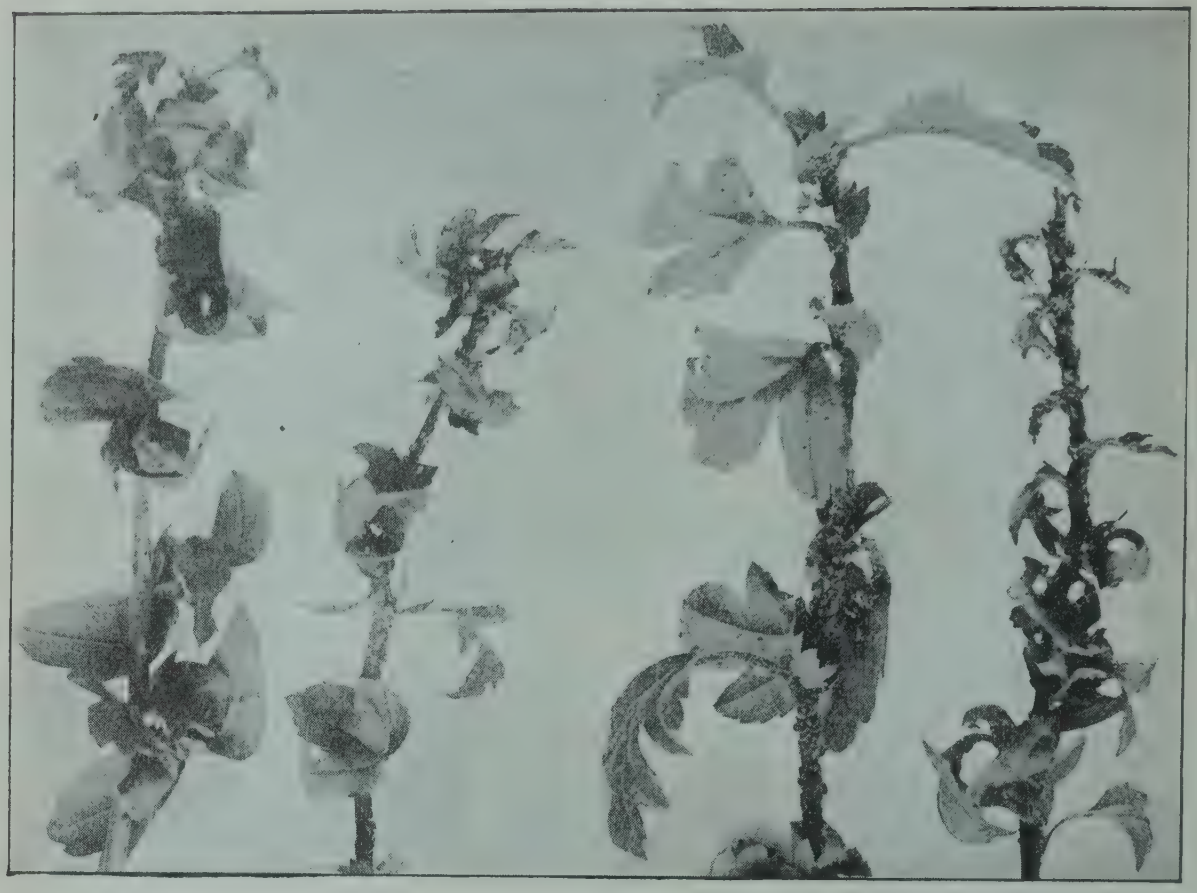


SPRING MIGRANTS OF APHIS SORBI ON A LEAF OF NARROW-LEAVED PLANTAIN



A NARROW-LEAVED PLANTAIN HEAVILY INFESTED WITH APHIS SORBI

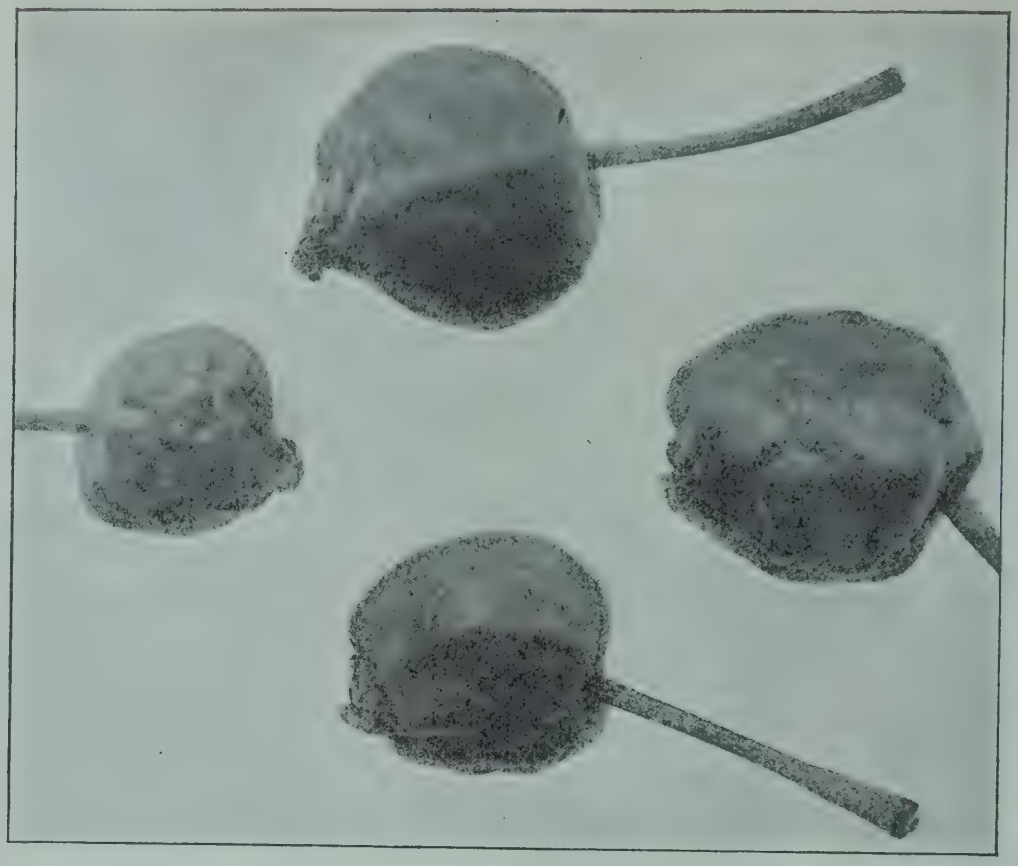
THE SAME PLANTAIN KILLED BY APHIS SORBI



VIGOROUS SHOOTS OF CRATAEGUS MONOGYNA ATTACKED BY APHIS POMI IN MIDSUMMER (JULY 19, 1918), SHOWING CURLING OF FOLIAGE

APHIS POMI SWARMING ON YOUNG TOMPKINS KING APPLES

APHIS POMI CLUSTERING ON LEAVES, FRUITSTALKS, AND FRUIT OF TOMPKINS KING APPLES (JULY 1). NATURAL SIZE



TOMPKINS KING APPLES SEVERELY INJURED BY APHIS POMI (JULY 4)

"CLUSTER FRUITS," OR "APHIS APPLES"

APHIS SORBI READY TO ATTACK THE FRUITS OF TWENTY OUNCE APPLES, AFTER SEVERELY CURLING THE LEAVES (MAY 31)

LEAVES OF TOMPKINS KING APPLES SEVERELY CURLED BY APHIS SORBI (MAY 27)

TIGHT LEAF ROLL CAUSED BY A SINGLE MOTHER AND A FEW YOUNG OF APHIS SORBI (MAY 25)

APPLE LEAF UNFOLDED TO SHOW A MASS OF APHIS SORBI

BALDWIN APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916).
NATURAL SIZE

FALL PIPPIN APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916). NATURAL SIZE

MAIDEN BLUSH APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916). NATURAL SIZE

being that of Britton (1910) and more recently those of Brittain (1915 b) and Baker and Turner (1916 b).

Altho this plant louse has been present for some time over a large section of the United States, it did not assume the status of an important apple pest until late in the nineteenth century. This is readily understood when it is considered that this species, in order to thrive, must have near at hand an abundance of its summer host plants, the narrow-leaved and broad-leaved plantains (*Plantago lanceolata* L. and *P. major* L.). From the writer's rearing experiments and field observations, it may be concluded that the narrow-leaved plantain (*P. lanceolata*) is the preferred host plant; in fact it appears to be essential, at least at Ithaca, to the continued reproduction of the species during the summer. Breeding experiments on broad-leaved plantains were never successful for more than two or three generations, the line dying off, sometimes very quickly. This agrees with the results of Baker and Turner (1916 b), altho Ross (1915) and Brittain (1916) report very successful breeding experiments on *P. major*.

### *Introduction and spread of summer host plants*

The two species of plantains *Plantago major* L. and *P. lanceolata* L. are importations from Europe. *P. major* appeared early, in all probability with the first permanent settlers in New England. Josselyn[4] records it as present in New England and following closely the habitats of the white settlers. So closely was it associated with the white man's coming that the Indians named it *Englishman's foot*, as tho it was produced by his treading. Bigelow[5] reports it as a common roadside weed in New England. Oakes[6] lists it as common about the houses and roadsides of Vermont. Since his time it has spread over the entire country. Its habitat is along beaten paths, by dusty roadsides, and in similar locations. In the northern sections of the United States and Canada there are two varieties, or perhaps good species, which possess thin leaves and occur in entirely different habitats. These are listed by Fernald[7] as *Plantago major* var. *intermedia*, which is found along salt

[4] Josselyn, John. New England's rarities discovered: in birds, beasts, fishes, serpents, and plants of that country, p. 1–114. 1672.

[5] Bigelow, Jacob. Florula Bostoniensis, p. 1–268. 1814.

[6] Oakes, Wm. Catalogue of Vermont plants. *In* History of Vermont, natural, civil, and statistical, by Zadock Thompson, part 1, p. 173–208. 1842.

[7] Fernald, Merritt L. Some recently introduced weeds. Massachusetts Hort. Soc. Trans. **1905**: 11–22. 1905.

marshes, and *P. major* var. *asiatica*, occurring along river banks and in moist situations thruout Canada and the northern United States.

The narrow-leaved plantain, *Plantago lanceolata*, is first recorded by Cutler[8] as not common in the meadows of New England. Bigelow[9] lists it as a common weed thruout the meadows of New England. Hitchcock[10] records it as prevalent in the meadows about Amherst, Massachusetts. Oakes[11] does not record it as present in Vermont, altho undoubtedly it must have reached southern Vermont at the date of his writing. The westward spread of *P. lanceolata* has been gradual and erratic. Hendrick[12] lists it from Onondaga County, New York, in 1834 and 1835. It is reported by Dewey[13] as being present in and about Rochester in 1841. Engelmann[14] does not record it as present in Illinois, tho only thirteen years later Lapham[15] reports it as one of the common plants there; evidently its introduction into Illinois was very widespread, due, of course, to the rapid opening up of the State. Winchell[16] observes that *P. major* is widespread in Michigan, whereas *P. lanceolata* is recorded from Ann Arbor only. Lapham[17] does not list *P. lanceolata* in his study of the flora of Wisconsin, and Upham[18] omits it from his list of the plants of Minnesota. Neither species is reported from central Colorado by Porter and Coulter[19], and Rydberg[20] states that both species are rare in the Rocky Mountain region. It is interesting to note that both species are first recorded from Oregon in 1896 as occurring on the Lander experimental farm, both undoubtedly having been introduced. Since that time

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[8] Cutler, Manasseh. An account of some of the vegetable productions, naturally growing in this part of America, botanically arranged. Amer. Acad. Arts and Sci. Memoir **1**:396–493. 1785.

[9] See footnote no 5, page 721.

[10] Hitchock, Edward. Catalogue of plants, growing without cultivation. *In* Report on the geology, mineralogy, botany, and zoology of Massachusetts, p. 599–651. 1833.

[11] See footnote no. 6, page 721.

[12] Hendrick, J. L. A catalogue of plants found growing chiefly in the vicinity of Onondaga Academy, collected during the summer of 1834 and 5. Regents Univ. State of New York. Ann. rept. **1837**:182–188. 1837.

[13] Dewey, Chester. Catalogue of plants, and their time of flowering, in and about the city of Rochester, for the year 1841. Regents Univ. State of New York. Ann. rept. **55**:265–272. 1842.

[14] Engelmann, George. Catalogue of a collection of plants made in Illinois and Missouri, by Charles A. Geyer. Amer. journ. sci. and arts **1**:**46**:94–104. 1844.

[15] Lapham, I. A. Catalogue of the plants of the State of Illinois. Illinois State Agr. Soc. Trans. **2**:492–550. 1857.

[16] Winchell, N. H. Catalogue of phaenogamous and acrogenous plants found growing wild in the lower peninsula of Michigan and the islands at the head of Lake Huron. Michigan Geol. Survey. Bien. rept. prog. **1**:245–330. 1861.

[17] Lapham, I. A. Plants of Wisconsin. Wisconsin State Agr. Soc. Trans. **2** (1852):375–419. 1853.

[18] Upham, Warren. Catalogue of the flora of Minnesota, including its phaenogamous and vascular cryptogamous plants, indigenous, naturalized, and adventive. Minnesota Geol. and Nat. Hist. Survey. Ann rept. **12** (1883)[6]:5–193. 1884.

[19] Porter, Thomas C., and Coulter, John M. Synopsis of the flora of Colorado. U. S. Geol. and Geog. Survey Terr. Misc. pub. 4:1–180. 1874.

[20] Rydberg, P. A. Flora of Colorado. Colorado Agr. Exp. Sta. Bul. 100:i–xxii, 1–448. 1906.

both species have spread to a considerable extent in the orchard sections of that and other Western States. P. A. Lehenbauer, Botanist of the University of Nevada, informs the writer that neither species is reported from Nevada, tho he thinks they may occur in some localities. It may be added that *Aphis sorbi* is not reported as being present in Nevada.

There is a remarkable parallelism between the introduction and spread of *Plantago lanceolata* and the spread and increasing destructiveness of *Aphis sorbi*. It has already been pointed out by the writer that this plant not only is the preferred, but seems to be the essential, summer host plant for this aphid. This statement is supported not only by experimental work but also by the study of the spread of the species. Had *Plantago major* been as favorable a summer host plant, the rosy aphis should have become abundant at an earlier date, as this plant was widely distributed thruout the country in advance of *Plantago lanceolata*. Had *Plantago major* var *asiatica*, a native thin-leaved variety found in Canada and the northern United States, been a favorable summer host plant, earlier outbreaks thruout the orchard areas of eastern Canada and the northeastern United States would have been expected. This is certainly not the case, as this aphis is first recorded as doing serious damage in the eastern United States and gradually working westward, northward, and southward in close relation with the spread of *Plantago lanceolata*. As has already been pointed out, neither species of plantain is abundant thruout the Rocky Mountain region. It is also well known that *Aphis sorbi* is not abundant nor seriously injurious in that region, except in certain restricted orchard sections where the narrow-leaved plantain has become well established. A very interesting situation is reported to the writer from British Columbia. In the coastal area *Aphis sorbi* has been abundant and destructive for a number of years, while in the interior valleys, where many of the larger orchards are found, this plant louse has appeared only in the last few years. *Plantago lanceolata* is reported by Macoun[21] as having been abundant in the coastal area since 1890, but it did not spread to the interior valleys until within the last few years. In consequence outbreaks of *Aphis sorbi* are now being reported from some of the larger orchard sections in the interior.

[21] Macoun, John. Catalogue of Canadian plants. Part II.—Gamopetalae, p. 193–394. Canada Geol and Nat. Hist. Survey. 1884.

Another interesting point in support of the above statement is the fact that *Plantago lanceolata* is primarily a plant of the meadows, thus providing ideal conditions for the development of *Aphis sorbi* in and about orchards. *Plantago major*, on the other hand, is a roadside weed, thick-leaved, sturdy, and well able to thrive under unfavorable conditions. Such a plant does not seem to be a favorable host for such a delicate insect as the summer forms of the rosy aphis.

## DISTRIBUTION

Altho the species *Aphis sorbi* was first recorded in Illinois in 1854, it is still difficult, owing to the confused condition of the literature, to state its exact distribution. It has been definitely recorded from Delaware, New Jersey, New York, Connecticut, Maine, Ohio, Oregon, and Colorado, and from various sections of Canada particularly in the apple-growing sections of Ontario, Nova Scotia, Quebec, and British Columbia. In all probability this plant louse is widely distributed in the apple-growing sections of the United States and Canada, but it has been so confused with *Aphis pomi* and *Aphis avenae* that it is hopeless to try to untangle the various brief references.

## NATURAL HISTORY

*Aphis sorbi*, like *Aphis pomi* and *Aphis avenae*, deposits its eggs on apple trees, and hibernation takes place, in the north at least, only in the egg stage. Hatching occurs early in the spring, about a week to ten days later than in the case of *Aphis avenae* and at about the same time as in *Aphis pomi*. For 1914 this was on April 26 and for 1915 on April 27. Close observations about Ithaca during the past three years clearly prove that comparatively few eggs of this species were deposited in this locality. As a result a very small number of the stem mothers were observed in the spring, yet, despite this fact, there was a severe infestation with serious loss of fruit in 1914, and there would also have been a similar condition in 1915 had there not been a timely application of adequate control measures.

Owing to the comparative rarity of the return migrants during the autumns of 1914 and 1915, very little work has been done on the egg stage of this species. The shy and wandering habits of the insects, combined with their scarcity, made futile any hopes for an adequate supply

of eggs. As a consequence no observations have been made on the failure of the eggs of this species to hatch due to the various factors which seem to play such a large part in the case of *Aphis pomi*.

*The stem mother*

The young, as soon as they hatch, actively seek out the opening buds of the apple, seeming to prefer the fruit buds. Under normal conditions close search has to be made for this species, as it usually occurs in very small numbers mingled among the abundant individuals of *Aphis pomi* and *A. avenae*. However, the whitish pulverulence, or powder, which covers its more or less dark purplish body readily serves as a distinguishing character. This pulverulent condition is especially marked after the second molt.

The stem mothers of this species differ considerably in their habits from those of the other two common species of apple aphids. As soon as the buds open, this species is most commonly found congregated about the opening flower buds; into these they penetrate, frequently attacking the flower stalks as the buds unfold. Some of the insects settle on the underside of the leaves, quickly causing them to curl.

The severe curling of the foliage caused by this species is in all probability the most characteristic feature of its work. A single stem mother located on the underside of a leaf near the midrib will cause the leaf to fold almost as tightly as the outer wrappings of a cigar (Plate XIV). As to the active agent which causes such a reaction on the part of the plant, scarcely anything is known. It requires the presence of only a few stem mothers to cause a severe curling of all the leaves surrounding an opening flower bud, and within such curls ideal protection is afforded to the rapidly developing plant lice. This work of curling the foliage so severely in the spring is due to this species alone; *Aphis pomi* causes only a partial folding, usually doing no more than bringing the tip and the base of the leaf into contact and never producing a close curl. Furthermore, *Aphis sorbi* is rarely found attacking the young and rapidly growing shoots, restricting itself to the foliage, the flower stalks, and the young fruit.

The stem mothers reach maturity at the time when the apple trees are coming into bloom. The blooming time varies from year to year, but in 1915 the first stem mothers became mature and began bringing forth young on May 10, just as the earliest blossoms were opening. In

1914 the earliest date on which stem mothers became mature was May 16 and this corresponded with the first unfolding of the blossoms.

The mature stem mothers are very inactive. They settle down and content themselves with pumping out the plant juices and producing young at a most phenomenal rate. When disturbed they quickly remove the proboscis from the plant tissues and seek out another spot in which to continue their operations.

*Reproductive period*

The stem mothers become mature in about two weeks after hatching, the length of time depends largely on weather conditions, tho under the most favorable circumstances nearly two weeks are required. The production of young usually begins in two or three days after the last molt, and continues without interruption for over a month. The stem mothers are remarkably hardy and their productive capacity is wonderful. As the warm, sunny days of spring come on, the plant louse seems to turn into a reproducing machine, and each morning the worker is filled with astonishment as he carefully removes and counts the overnight progeny, seemingly greater in bulk than that of the mother. This rate of production continues day after day, as may be seen by consulting Reproduction Chart II. In these experiments the average daily production thruout the productive period was 5.45 for four individuals. The greatest number produced in one day was 33, while the average length of the productive period was 33.5 days. The total production of young by the various individuals varied from 131 to 244, with an average of 184.

In the case of this species the period of reproduction extends from about May 10 to June 20 or later. As the eggs of this species hatch over a period of ten or more days, undoubtedly the last stem mothers to hatch are still producing during the last week of June. However, the maximum period of productive activity is during the last week of May and the first week of June, that is, while the young fruits are beginning to set and start active growth.

*Description of stages*

*First instar* (Plate XVIII).— Average length 0.6 mm.; average width 0.3 mm. (There is considerable variation in these measurements, dependent on the age of this instar.)

A B C

FIRST INSTARS OF STEM MOTHERS

A, Aphis pomi; B, Aphis sorbi; C, Aphis avenae. All drawn to same scale

APHIS POMI. MATURE STEM MOTHER. × 60

APHIS SORBI, MATURE STEM MOTHER. × 60

APHIS AVENAE, MATURE STEM MOTHER. × 60

APHIS POMI, WINGED VIVIPAROUS FEMALE, THIRD GENERATION

APHIS POMI, MATURE OVIPAROUS FEMALE

APHIS POMI, MATURE MALE

APHIS SORBI, SPRING MIGRANT TO NARROW-LEAVED PLANTAIN

APHIS SORBI, RETURN MIGRANT FROM PLANTAIN TO APPLE

APHIS SORBI, MATURE OVIPAROUS FEMALE

APHIS AVENAE, SPRING MIGRANT FROM APPLE TO GRAINS AND GRASSES

APHIS AVENAE, FALL MIGRANT FROM GRAINS AND GRASSES TO APPLES

APHIS AVENAE, MATURE OVIPAROUS FEMALE

Reproductive Chart II. Aphis sorbi

## REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of third generation, apterous female, 1915

| No. | June | | | | | | | | | | | | | | | | | July | | | | | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | | | | | | | | | | | | | | | | | |
| 141 | .. | .. | 8 | 8 | 6 | 8 | 12 | 5 | 10 | 5 | 6 | 7 | 4 | 6 | 6 | 6 | 7 | 8 | 6 | 7 | 3 | 1 | 1 | 1 | 0 | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | |
| 142 | .. | 2 | 7 | 6 | 8 | 5 | 21 | 5 | 10 | 6 | 5 | 4 | 8 | 5 | 10 | 8 | 8 | 7 | 2 | 3 | 2 | 2 | 1 | 0 | 0 | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | | 22 | 5.95 | 12 | 131 | July 10 | 36 |
| 143 | .. | .. | .. | .. | 5 | 8 | 10 | 7 | 7 | 5 | 10 | 3 | 8 | 5 | 4 | 8 | 10 | 7 | 10 | 7 | 9 | 4 | 1 | 1 | .. | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | | 22 | 6.14 | 21 | 135 | July 12 | 39 |
| 149 | .. | .. | .. | .. | 7 | 9 | 7 | 5 | 2 | 8 | 5 | 5 | 7 | 4 | 7 | 8 | 16 | 5 | 8 | 5 | 5 | 3 | 5 | 0 | 1 | 1 | 1 | 0 | 0 | | | | | | | | | | | | | | | | | | | 20 | 6.45 | 10 | 129 | July 30 | 55 |
| 152 | 4 | 6 | 9 | 2 | 12 | 9 | 8 | 4 | 6 | 2 | 1 | 5 | 4 | 2 | 1 | 7 | 6 | 3 | 5 | 7 | 3 | 3 | 0 | 6 | 2 | 1 | 0 | 0 | .. | | | | | | | | | | | | | | | | | | | 23 | 5.39 | 16 | 124 | July 18 | 43 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 | 4.54 | 12 | 118 | July 17 | 46 |
| Averages ..... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 22.6 | 5.69 | | 127.4 | | 43.8 |

Reproductive capacity of winged migrant (spring). 1917

| No. | June | | | | July | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | | | | | | | | | | | | | | | | | | |
| 305 | 11 | .. | .. | .. | .. | .. | .. | .. | 14 | .. | 2 | .. | 1 | .. | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | |
| 306 | 6 | .. | .. | .. | .. | .. | .. | .. | 15 | .. | 4 | .. | 6 | .. | 1 | .. | .. | .. | .. | .. | .. | .. | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | |
| 309 | 12 | .. | .. | .. | .. | .. | .. | .. | 9 | .. | 4 | .. | 0 | .. | 1 | .. | .. | 1 | .. | 0 | .. | 0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | | 15 | 1.8 | ..... | 28 | July 14 | 30 |
| 312 | 15 | .. | .. | .. | .. | .. | .. | .. | 9 | .. | 5 | .. | 5 | .. | 2 | .. | .. | 3 | .. | 0 | .. | 0 | .. | 0 | .. | .. | .. | .. | .. | .. | .. | .. | | | | | | | | | | | | | | | | | | | 20 | 1.65 | ..... | 33 | July 23 | 39 |
| 313 | 10 | .. | .. | .. | .. | .. | .. | .. | 17 | .. | 2 | .. | 2 | .. | 0 | .. | .. | 3 | .. | 1 | .. | 0 | .. | 0 | .. | 0 | .. | 1 | .. | 2 | .. | 2 | | | | | | | | | | | | | | | | | | | 20 | 1.35 | ..... | 27 | July 19 | 35 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 20 | 1.95 | ..... | 39 | July 28 | 44 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 34 | 1.18 | ..... | 40 | July 28 | 44 |
| Averages ..... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 21.8 | 1.60 | | 33.4 | ..... | 38.4 |

## REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of second generation, apterous female on plantain, 1917

| No. | July | | | | | | | | | | | | | | | | | | | | | | | August | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | | | | | |
| 317 | 7 | | 5 | | 7 | | | 10 | | | 7 | | 13 | | 8 | | 11 | | 9 | | | 9 | | 3 | | 3 | | | 1 | | 1 | | 1 | | | | | | | 34 | 2.79 | | 95 | Aug. 20 | 58 |
| 319 | | | 3 | | 8 | | | 8 | | | 10 | | 4 | | 9 | | 13 | | 12 | | | 4 | | | | | | | | | | | | | | | | | 22 | 3.23 | | 71 | July 30 | 33 |
| 320 | | | 6 | | 7 | | | 10 | | | 9 | | 5 | | 10 | | 9 | | 6 | | | 12 | | 2 | | 1 | | | | | | | | | | | | | 26 | 2.96 | | 77 | Aug. 4 | 40 |
| 321 | | | 6 | | 6 | | | 9 | | | 8 | | 10 | | 6 | | 10 | | 7 | | | 11 | | 3 | | 3 | | | 2 | | 1 | | 0 | | | | | | 31 | 2.61 | | 82 | Aug. 20 | 56 |
| 323 | | | 5 | | 6 | | | 9 | | | 2 | | 0 | | 8 | | 7 | | 6 | | | 14 | | 10 | | 7 | | | 5 | | | | | | | | | | | 29 | 2.72 | | 79 | Aug. 6 | 42 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Averages ..... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 28.4 | 2.87 | | 80.8 | | 45.8 |

Reproductive capacity of third generation, apterous female on plantain, 1917

| No. | July | | | | | | | | | | | August | | | | | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | | | | | | | | | | | | |
| 326 | 3 | | 5 | | 7 | | | 14 | | 11 | | 17 | | | 6 | | 3 | | 7 | | | 4 | | 0 | | 5 | | | 1 | | 0 | | | | | | | | | 29 | 2.86 | | 83 | Aug. 29 | 49 |
| 327 | 4 | | 2 | | 9 | | | 13 | | 8 | | 14 | | | 12 | | 3 | | 7 | | | 6 | | | | | | | | | | | | | | | | | 19 | 3.79 | | 72 | Aug. 11 | 33 |
| 328 | 2 | | 4 | | 6 | | | 8 | | 8 | | 5 | | | 12 | | 6 | | 5 | | | 8 | | 5 | | 4 | | | 2 | | 0 | | 0 | | | | | 31 | 2.55 | | 79 | Sept. 5 | 47 |
| 331 | | | 5 | | 9 | | | 16 | | 4 | | 10 | | | 10 | | 5 | | 5 | | | 5 | | 2 | | 1 | | | 0 | | 1 | | 0 | | | | | 30 | 2.37 | | 71 | Sept. 8 | 61 |
| 334 | | | 4 | | 11 | | | 13 | | 8 | | 10 | | | 7 | | 6 | | 5 | | | 6 | | 4 | | 1 | | | 5 | | 0 | | 0 | | | | | 28 | 2.86 | | 80 | Aug. 29 | 50 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Averages ..... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 27.4 | 2.89 | | 77 | | 48 |

## REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of fourth generation, apterous female on plantain, 1917

| No. | August | | | | | | | | | | | | | | | | | | | | | | | | | | | | | September | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | | | | | |
| 342 | 4 | | | 6 | | 5 | | 7 | | | 11 | | 5 | | 9 | | | 9 | | 5 | | 6 | | | 2 | | 1 | | 0 | | | | | | | | | | | | | | 27 | 2.59 | | 70 | Sept. 1 | 42 |
| 343 | 2 | | | 6 | | 4 | | 5 | | | 6 | | 6 | | 5 | | | 11 | | 7 | | 7 | | | 7 | | 0 | | | | | | | | | | | | | | 25 | 2.64 | | 66 | Sept. 22 | 63 |
| 344 | 2 | | | 3 | | 6 | | 3 | | | 7 | | 5 | | 3 | | | 3 | | 4 | | 4 | | | 9 | | 6 | | 3 | | | | | | | | | | | | | 32 | 1.91 | | 61 | Sept. 3 | 44 |
| 349 | | | | 2 | | 5 | | 5 | | | 8 | | 2 | | 8 | | | 5 | | 5 | | 6 | | | 7 | | 3 | | 4 | | | 3 | | 0 | | | | | | | 36 | 1.72 | | 62 | Sept. 10 | 48 |
| 350 | | | | 2 | | 4 | | 3 | | | 4 | | 4 | | 5 | | | 7 | | 3 | | 5 | | | 5 | | 2 | | 3 | | | 1 | | 0 | | 0 | | 1 | | 1 | *a* | 47 | 1.25 | | 59 | Sept. 29 | 67 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | 33.4 | 2.02 | | 63.6 | | 52.8 |

*a* 1 on September 12, 15, and 19, respectively.



Reproductive capacity of fifth generation, apterous female on plantain, 1917

| No. | August | | | | | | | | | | | September | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | | | | | | | | | |
| 359 | 3 | | 3 | | | 15 | | 5 | | 4 | | | 4 | | 7 | | 2 | | | 3 | | 1 | | 0 | | | 0 | | 1 | | 0 | | | | | | | | | | | 29 | 1.65 | | 48 | Sept. 19 | 44 |
| 362 | 1 | | 6 | | | 9 | | 6 | | 6 | | | 6 | | 5 | | 2 | | | 3 | | 0 | | 2 | | | 2 | | 2 | | 5 | | | 3 | | 0 | | 3 | *b* | | | 41 | 1.56 | | 64 | Oct. 1 | 55 |
| 364 | | | 3 | | | 9 | | 6 | | 5 | | | 14 | | 4 | | 3 | | | 1 | | 0 | | | | | | | | | | | | | | | | | | | 18 | 2.50 | | 45 | Sept. 12 | 36 |
| 366 | | | | | | 4 | | 4 | | 5 | | | 10 | | 6 | | 0 | | | 3 | | 3 | | 0 | | | 6 | | 3 | | 4 | | | 2 | | 2 | | 5 | *c* | | | 40 | 1.50 | | 60 | Oct. 15 | 66 |
| 367 | | | | | | 2 | | 3 | | 4 | | | 12 | | 6 | | 0 | | | 2 | | 1 | | 0 | | | 3 | | 2 | | 1 | | | 2 | | 1 | | 1 | *d* | | | 43 | 1.05 | | 45 | Oct. 21 | 72 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Averages | 34.2 | 1.65 | | 52.4 | | 54.6 |

*b* 3 on September 29.
*c* 1 on September 29, October 1, and October 3, respectively.
*d* 4 on September 29, 1 on October 6.

## REPRODUCTION CHART II. APHIS SORBI (*concluded*)

Reproductive capacity of sixth generation, apterous female on plantain, 1917

| No. | September | | | | | | | | | | | | | | | | | | | | | | | | | October | | | | | | | | | | | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | | | | | | |
| 376 | 2 | | | 4 | | 2 2 | | 2 2 | | | 3 1 | | 4 | | 2 | | | 6 | | 3 | | 4 | | | 4 | | 3 | | 1 | | 4 | | 2 | | 0 | | | 2 | | 0 | *e* | 47 | 1.17 | | 55 | Nov. 5 | 75 |
| 377 | | | | 4 | | 2 2 | | 2 2 | | | 3 2 | | 3 | | 4 | | | 5 | | 2 | | 2 | | | 6 | | 3 | | 3 | | 2 | | 1 | | 1 | | | 1 | | 0 | *f* | 52 | 1.00 | | 52 | Oct. 29 | 66 |
| 379 | | | | | | 2 | | 1 | | | | | 2 | | 2 | | | 7 | | 2 | | 2 | | | 6 | | 0 | | 2 | | 3 | | 2 | | 1 | | | 0 | | 0 | *g* | 57 | 0.77 | | 44 | Nov. 16 | 81 |
| 380 | | | | | | 4 | | 1 | | | 3 | | 0 | | 3 | | | 3 | | 0 | | 4 | | | 6 | | 4 | | 1 | | 5 | | 1 | | 0 | | | 0 | | 0 | *h* | 43 | 0.90 | | 38 | Nov. 4 | 70 |
| 381 | | | | 2 | | 2 | | 1 | | | 4 | | 5 | | 2 | | | 6 | | 1 | | 5 | | | 4 | | 3 | | 4 | | 2 | | 0 | | 0 | | | 2 | | 0 | *i* | 52 | 0.94 | | 49 | Nov. 5 | 72 |
| Averages | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 50.0 | 0.96 | | 47.6 | | 72.8 |

*e* 3 on October 21.
*f* 3 on October 21, 1 on October 29.
*g* 3 on October 21, 1 on October 29, 2 on November 5.
*h* 3 on October 17, 1 on October 21.
*i* 5 on October 21, 1 on October 29.



Reproductive capacity of seventh generation, winged female on apple (fall migrant), 1917

| No. | October | | | | | | | | | | | | | | | | | | | | | | | | | | November | | | | | Productive period (days) | Average daily production | Greatest number produced in one day | Total number of young | Date of death | Total length of life (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 1 | 2 | 3 | 4 | 5 | | | | | | | | | | | | | | |
| 543 | 9 | | | | 2 | | | 0 | | | | 3 | | | | 1 | | | | | | | | | | | | | | | | | 18 | 0.83 | | 15 | Oct. 21 | 34 |
| 544 | 9 | | | | 1 | | | 0 | | | | 0 | | | | | | | | | | | | | | | | | | | | | 7 | 1.43 | | 10 | Oct. 17 | 30 |
| 545 | 9 | | | | 2 | | | 1 | | | | 0 | | | | 0 | | | | | | | | 0 | | | | | | 1 | | | 29 | 0.45 | | 13 | Nov. 16 | 60 |
| 546 | 12 | | | | 2 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 10 | 1.50 | | 15 | Oct. 17 | 30 |
| 547 | 9 | | | | 0 | | | 3 | | | | 0 | | | | 1 | | | | | | | | 1 | | | | | | | | | 26 | 0.54 | | 14 | Nov. 5 | 51 |
| Averages | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 18 | 0.95 | | 13.4 | | 41 |

The general color is dark green, with a row of small black spots on each side of the median dorsal line; the antennae, the eyes, two large quadrate areas on the dorsal surface of the head, the legs, and the cornicles are black. The sides of the body show a distinct whitish pulverulence especially toward the end of the instar; the ventral surface is covered with a marked white pulverulence. The cornicles (fig. 111, B, page 684) are long and cylindrical, constricted before the apex, which is distinctly flanged. The antennae are 4-segmented, long, reaching about halfway between the end of the thorax and the base of the cornicles; the unguis is more than twice as long as the basal part of the segment (fig. 111, B page 684).

*Second instar.*— The second instar does not differ in any respect from the first except as to size. The whitish pulverulence, however, is more pronounced.

*Third instar.*— Length 1.44–1.52 mm.; width 0.72 mm.

The coloration varies greatly, not only in different individuals but in the same individual, during this instar; in general the dorsal surface is yellowish green mottled with yellow; the sides are darker green, and completely covered with a fine white pulverulence; around the base of the cornicles and between them the color is reddish brown to red. The head is dark, with two tubercles on the hind margin. The antennae are 5-jointed, pale on the basal third, on the remainder dusky to black. The eyes are prominent and black. The cornicles are cylindrical, slightly flaring at their tips, brownish to black. There are pointed, black, lateral tubercles on the prothoracic segment and on all the abdominal segments except the last two; on the last two abdominal segments are black bands bearing a tubercle on each side of the median line. The cauda is scarcely visible, black. The legs are dusky to black. The ventral surface is covered with a beautiful white pulverulence.

*Fourth instar.*— Length 1.9 mm.; width 1.04 mm.

The general coloration is the same as for the preceding instar, but with a tinge of bluish in the greenish ground color. The entire body is covered with a beautiful white pulverulence. The antennae are 6-jointed. There are no other differences between this and the preceding instar.

*Fifth instar, mature stem mother* (Plate XX).— Length 2.25 mm.; width 1.44 mm.

The body is broadly pear-shaped, tending to globular in older specimens. The coloration varies greatly, not only in different individuals but also in the same individual during its life; in general the abdomen is yellowish green mingled with purplish brown, the sides being usually dark purplish brown; the head and the thorax are dark brown tending to purplish; around the cornicles and between them the color is often reddish; the legs are yellowish, with the femora, the distal ends of the tibiae, and the tarsi, fuscous to black. The entire body is covered with a fine white pulverulence. The head bears two short tubercles on the vertex. The eyes are black. The prothorax bears a pair of black dorsal tubercles as well as a lateral tubercle on each side. The remaining thoracic segment, and each of the first six abdominal segments, bear a pair of black lateral tubercles; the seventh and eighth abdominal segments, each have a transverse, dorsal, chitinous plate bearing two pointed tubercles, one on each side of the median line. The antennae are 6-jointed, fuscous at the base with the remainder black. The length and number of sensoria of the segments (fig. 112, c, page 685) are as follows: Segment III, 0.32 mm., sensoria 0; Segment IV, 0.24 mm., sensoria 0; Segment V, 0.22 mm., sensoria 1; Segment VI, 0.1 mm. + 0.22 mm., sensoria the usual group.

*The second generation*

In 1915 the first young were produced by the stem mothers on May 11 and reached maturity on May 26. In general the second generation required from fourteen to twenty days to reach maturity and begin to produce young.

One of the most characteristic features of this species is the congregation of the young about the mother. Each individual stem mother or group of mothers will have massed about it hundreds of young, so that the infested leaves may be so covered as to be actually more than one layer deep (Plate XIV). This gregarious habit soon causes the death of the infested leaves and the consequent migration of the aphids. However, when several stem mothers congregate on a single leaf, forced migration soon follows owing to the lack of available space. The young move actively and hurriedly, seemingly anxious to locate a suitable feeding ground. It is at this period that they are so frequently found congregated on the forming fruits or attacking the new and succulent unfolding foliage.

The majority of this generation are wingless females; at least this has been the case in the writer's rearing experiments. In the field considerable numbers of winged forms developed, about 25 per cent so far as the writer could judge. These undoubtedly migrated to the summer food plant, tho no direct observations were made in the field. In cage experiments the winged forms readily reproduced on plantain as well as on apple.

*Reproductive capacity*

The second generation begins active reproduction during the last few days of May and reaches its maximum about the middle of June. The length of the individual productive period varies from 20 to 32 days, the average being 25 days. As the stem mothers continue reproducing until the latter part of June, the productive period of the second generation extends from the last few days of May until about the middle of July, the maximum reproduction occurring about the middle of June or slightly later. The average daily production (4.68) is lower than that of the stem mother, and the total production of each individual (average 119.2) is much less.

*Description of stages*

*First instar.*— Length 0.8 mm.; width 0.44 mm.; cornicles 0.08 mm. long. The young, when just born, are light cream-color thruout and are very active. The antennae and the legs are long, giving the young insect a sprawling appearance. The eyes are at first reddish but soon turn black. The distal ends of the tibiae and the tarsi become black shortly after the insect hatches. The entire body soon becomes covered with a delicate white pulverulence. The length of this instar is 2+ days.

*Second instar.*— Length 1 mm.; width 0.5 mm.; cornicles 0.12 mm. long. The general color and markings are similar to those of the first instar; there is a faint tinge of red in the yellowish ground coloring, otherwise no difference can be observed. The length of this instar is 2+ days.

*Third instar.*— Length 1.2 mm.; width 0.8 mm.; cornicles 0.2 mm. long. The general color is yellowish, with the sides of the abdomen around the bases and between the cornicles reddish; the head is somewhat dusky. The entire body is covered with a fine white pulverulence. The antennae are 6-jointed, with the basal half yellowish and the remainder black.

The cornicles are cylindrical, black, slightly flaring at the tips. The legs are yellowish, with the distal ends of the tibiae and the tarsi black. Black lateral tubercles are present on the prothorax and on the first six abdominal segments; the seventh and eighth segments each bear a pair of small black tubercles, one on each side of the median line. The length of this instar is 4+ days.

*Fourth instar.*— Length 1.6 mm.; width 0.9 mm.; cornicles 0.28 mm. long.

The general color is yellowish, with pink or reddish on the sides and around and between the cornicles. The whole body is covered with a delicate white pulverulence. The antennae are 6-jointed, fuscous. The legs are yellowish, except for the distal ends of the tibiae and the tarsi, which are fuscous to black. Small black lateral tubercles are present on the prothorax and on the first six abdominal segments; on the seventh and on the eighth abdominal segment is a pair of small dorsal tubercles, one on each side of the median line. Thele ngth of this instar is 4+ days.

*Fifth instar.*— Mature apterous viviparous female.—Length 1.84 mm.; width 1.04 mm.; cornicles 0.36–0.4 mm. long.

The recently molted female is dark purplish brown to olivaceous in color, with considerable spotting of light greenish on the dorsal part of the abdomen; the central part of the head and the anterior margin of the prothorax are yellowish; around the base of the cornicles and on a broad band between them the color is reddish. The entire body is covered with a beautiful white pulverulence. The cornicles are cylindrical, slightly tapering, flaring at their tips; the color is reddish yellow on the basal part, with the distal half black. The antennae are 6-jointed; the basal half is lemon-yellow, the distal half fuscous to black. The eyes are black and tuberculate. The legs are yellowish, with the distal ends of the femora, the tibiae, and the tarsi fuscous to black. Lateral tubercles are present on the prothorax and on all the abdominal segments except the seventh and the eighth; the last-named bear small dorsal tubercles, one on each side of the median line.

The apterous females vary greatly in coloration. The commoner form is the one just described. All gradations, to the form described as follows, may be discovered by a close examination of a wide series of individuals: general color yellowish, the sides faintly tinged with pink or reddish; around the cornicles, and a band between, dark red; basal half of

antenna yellow, remainder black; legs yellow, the distal ends of the tibiae, and the tarsi, black; cornicles yellow, tips black.

Winged viviparous female.— Length 1.44 mm.; width 0.8 mm.; cornicles 0.24 mm. long; wing expanse 5–6 mm.

The head is black, with the tubercles on the vertex prominent. The eyes are red to almost black, and tuberculate. The antennae are 6-jointed; the color is black except for the two basal segments, which are fuscous. The thorax is shining black. The base of the femora is banded with yellowish, the remainder is black; the tibiae are yellowish brown, with the distal ends black; the tarsi are black. The abdomen is yellowish brown at the sides and the base, with the dorsal part fuscous to black; around and between the cornicles the color is reddish yellow. The cornicles are cylindrical, gradually tapering, somewhat flared at the tips, black. The cauda is short and fuscous. Lateral tubercles are present on the prothorax and on all the abdominal segments except the seventh and the eighth, each of which bears two dorsal tubercles, one on each side of the median line.

*The third generation*

In 1915 the descendants of the second generation — that is, the third generation — began reaching maturity on June 12. In the writer's large rearing cage, where the seedling trees had become very crowded with the plant lice, the majority of the insects, in fact nearly all, acquired wings and migrated to their summer food plant. However, many did not acquire wings and these began producing another generation on the apple. The writer's observations in the field during the past season (1917) led to the conclusion that the majority of the lice of this generation did not acquire wings but settled down and produced a fourth generation on the apple. When such conditions occur there results a serious infestation, with consequent damage to foliage and fruit.

In 1915 the wingless females of the third generation began producing young on June 12, and the productive period extended well into July. In the case of five normal individuals the average producing period was 22.6 days, while the daily production averaged 5.69. The productive capacity averaged 127.4, which is considerably lower than that of the stem mothers but somewhat higher than that of the second generation.

The habits and activities of the third generation do not differ from

those of the second. The lice congregate in immense numbers on the underside of the foliage, causing severe curling; they also attack the setting and developing fruit, producing their characteristic injuries which are described later. At Ithaca in 1915, the majority of this generation acquired wings and migrated to their summer host plants.

When the last skin is shed the winged adults are very tender and inactive. They remain secreted in the curled leaves for several days, generally two or three, before venturing on their migratory flight. They then become very active and nervous, running about or moving their wings up and down in anticipation of their flight. What factors influence the production of winged or wingless forms in this generation can only be conjectured. In cage experiments where in some cases crowding became excessive, practically all of this generation acquired wings; whereas under similar conditions in other cages many of the insects did not acquire wings and produced a fourth generation on the apple. Many theories have been advanced, based entirely on observation, as to the influence which climatic factors, such as heat, cold, or moisture, may have; excessive crowding also has been used very generally in explaining the early production of winged forms. Unfortunately, thru lack of equipment no experiments could be undertaken by the writer to determine the influence of any of the factors involved. The importance and significance of the development of the winged migrants in any particular generation are very great, not only to the biologist, but also, and more particularly, to the orchardist. This is pointed out in more detail in the discussion of the summer migration of this species.

*Description of stages*

The early instars of the third generation are practically identical with those of the second generation, both in size and in color markings. It will therefore be sufficient to describe only the last two instars of this generation, restricting the description to the winged forms; the wingless forms are practically identical with those of the preceding generation and require no special description.

*Fourth instar, winged female.*— Length 1.8–2 mm.; width 0.9–1 mm.; cornicles 0.26–0.28 mm. long.

The general color after the molt is a bright pink, which gradually changes to a rusty reddish over the entire abdomen, the wing pads shading to

a reddish yellow; the head, the distal half of the antennae, the cornicles, and the distal ends of tibiae and tarsi, are black; the femora and the proximal parts of the tibiae are yellow. The entire body is covered with a rather dense white pulverulence. The lateral and caudal tubercles are present and appear as small dark spots.

*Fifth instar, mature winged female (spring migrant)* (Plate XXIV).—Length 1.44–2 mm.; width (wing expanse) 5–6 mm.; cornicles 0.32–0.38 mm. long.

The head is black above, with the median ocellus protruding and appearing as a tubercle. The antennae, the dorsal part of the thorax, a large quadrate area on the dorsum of the abdomen, the cornicles, the distal half of the femora, the distal ends of the tibiae, and the tarsi, are black; the proximal ends of the femora, and the tibiae except the tips, are yellowish brown; on each lateral margin of the abdomen in front of the cornicles are three rounded black areas; in front of the large quadrate black spot on the abdomen there are narrow transverse black lines in some specimens, but these are frequently lacking; around the base of the cornicles the color is black, and this is often fused with the black quadrate areas; the remainder of the body is of a yellowish brown color. The wings are hyaline, with the veins thin and the stigma dusky. The eyes are tuberculate and black; on the vertex between them is a pair of small tubercles. The prothorax has a prominent tubercle on each side. The abdomen has small but distinct lateral tubercles and prominent dorsal tubercles on the last two segments. The cauda is conical, short, setose, and provided with two or three pairs of long curving hairs. The cornicles are cylindrical, faintly imbricated, curved, and distinctly flanged on the distal end (fig. 115, c, page 706).

The antennae (fig. 114, c, page 705) are 6-jointed. Segments I and II are imbricated on their inner margins and armed with a few short, sharp spines; Segment III has numerous sensoria, varying from 50 to 60, the imbrications showing faintly; Segment IV is similar to Segment III, but bears only about half the number of sensoria, varying from 20 to 30; Segment V has only from 4 to 10 sensoria, and the imbrications are more distinct; Segment VI is strongly imbricated, and the unguis is short and bears the usual group of sensoria at its distal end. The length of the segments is as follows: Segment III, 0.6–0.7 mm.; Segment IV, 0.44 mm.; Segment V, 0.28 mm.; Segment VI, 0.12 + 0.56 mm.

*The fourth generation*

Altho the majority of the third generation under experimental observation acquired wings, a goodly number were wingless and were easily induced to continue reproducing on the apple. Their young constitute the fourth generation on apple.

The habits and activities of this generation do not differ in any respect from those of the third. The leaves, especially those about the fruit clusters, become crowded by the lice, which swarm also on the developing fruits. In 1915 they began reaching maturity about June 25, and from that date to the middle of July large numbers of winged forms were present on the apple trees. All those under experimental conditions acquired wings, and in the field, so far as could be learned by constant observation, all of this generation became winged and constituted the main spring migration of the years 1915 and 1917.

As the nymphal stages are practically identical with those of the second and third generations, it is not necessary to repeat detailed descriptions. The adult corresponds so closely to that of the third generation that the description of the winged female of that generation will serve in this case.

*The migratory forms*

At Ithaca the migratory forms of *Aphis sorbi* may consist of the winged females of either the second, the third, or the fourth generation (counting the stem mothers as the first generation). At Vienna, Georgia, Baker and Turner (1916 b) found that the migratory forms may appear in every generation from the third to the eighth on the apple. The writer did not succeed in rearing more than four generations on the apple, tho repeated attempts were made. However, from field observations and from notes in the files of the Department of Entomology at Cornell University, it would appear that in some years there are undoubtedly more than four generations in certain sections of New York State. As yet there are no definite data to prove or disprove such a belief. Brittain (1915 b) finds that in Nova Scotia the migratory forms are the winged adults of the third generation. He reports, however, that in individual rearing experiments, in which the number of plant lice to each seedling was very small, he succeeded in rearing a total of seven generations on the apple. In some experiments no migrants were produced. Brittain does not state

the number of generations of the latter that were reared. In the spring of 1915 the main migration at Ithaca consisted of the adults of the fourth generation, tho a large proportion of the third generation also migrated to the summer food plants. In 1916 there was only a slight infestation about Ithaca and practically all of the third generation consisted of the winged migratory forms.

The factors which influence the early or late production of migratory forms have not been suggested by any worker. The necessity of investigating the influence of climatic factors is urgent. As has already been pointed out, this is a very interesting problem to the biologist, and to the fruit grower it is one of paramount importance. In 1915 there was a serious outbreak of *Aphis sorbi* in New York State and the amount of damage done was very great. This was largely due to the fact that a comparatively small proportion of the third generation produced migrants. As a result the enormous numbers of the third generation produced young at a very rapid rate, resulting in the most serious infestations. The writer saw an orchard which, about the early part of June, showed only the usual marginal infestation in the lower branches. In this case the third generation (young) was appearing in large numbers and it was thought most of them would become migrants. For some unknown reason scarcely any of these produced winged forms, and as a result the trees became so infested that scarcely a leaf or a fruit could be found that was not crowded with the lice. When this generation (the fourth) became nearly mature there was not sufficient nourishment for them and they migrated in thousands to the branches and trunks, while the ground under the trees was literally swarming with them. As this orchard was well cultivated, the majority of the aphids died, tho thousands reached maturity and migrated to adjacent fields where the narrow-leaved plantain was growing in abundance. In this one small orchard the owner estimated his loss at from $800 to $1000. If the factors involved in the early or the late production of the winged migrants could be determined, this would be a long step in solving some problems in insect control.

There is another important point which cannot be overlooked at this time. Ross (1915) reports that he succeeded in rearing this species thruout the season on apple in Ontario, Canada, tho he presents no definite data. If this condition should become prevalent, there would be an instance

of a species that normally migrates to a summer host plant gradually acquiring the ability to reproduce continuously on its primary host. The production of a maximum of eight broods on apple at Vienna, Georgia, and the rearing experiments of Brittain (1915 b), would lend support to Ross's experimental work.

Another point of considerable importance is whether, during the summer, winged or wingless forms on plantain can migrate to apple and produce generations thereon. Brittain (1915 b) succeeded in one case in making such a transfer, using the progeny of the fourth generation on plantain. These matured and produced young which developed into the plantain forms. The writer has not succeeded in making such transfers, but in 1915 an infestation of this aphid was found on a Northern Spy on August 5. At that time only a few leaves were infested, and developing young, both winged and wingless, were present. This infestation became severe by August 25, but shortly thereafter all the aphids transformed to winged individuals and left the tree. Where this infestation came from is a mystery, as no lice had been present early in the season, and moreover the tree had been thoroly sprayed at least twice with Black-leaf-40 tobacco extract and soap. Neighboring apple trees had not a single plant louse present, nor did any lice appear later in the season. All about these trees there was a very abundant growth of narrow-leaved plantain, but no lice could be found on them at the time of the first appearance of the infestation on the Northern Spy tree.

*Habits of the migratory forms*

The spring migratory forms are very lively, and in the rearing cages they fly actively about, particularly in the bright sunshine. In the cages inclosed with cheesecloth they congregated in large numbers on the sunniest side and seemed very strongly attracted to the light. They would walk actively about, opening and shutting their wings, and seemed to be tiptoeing gently across the cloth in a very nervous manner. Gradually they discovered the narrow-leaved plantains in the cages (Plate VIII) and settled on them. Altho several broad-leaved plantains were also present they left these alone. Usually within from two to three days these winged forms began producing young, and then they became much more quiescent while their broods of young congregated closely about them.

*The summer host plants*

For many years the summer host plants have been searched for in vain. It remained for Ross (1915) to first record his successful transfer experiments to the broad- and narrow-leaved plantains (*Plantago major* and *P. lanceolata*). He states also that this species was reared thruout the summer on apple where crowding was prevented.

The experiments of the writer prove that at Ithaca the narrow-leaved plantain, or rib grass (*P. lanceolata*), is the preferred summer host plant and also in all probability the necessary summer host plant. In numerous experiments this species of lice could be reared on *P. major* for only two or three generations, when the line would die out, due to unknown causes; whereas under similar conditions the insects would continue to thrive on *P. lanceolata*. The results of these experiments are in accord with the work of Baker and Turner (1916 b), tho not with that of Ross (1915 and 1916) and of Brittain (1915 b). The more important reasons for believing that *P. lanceolata* is the necessary host plant, and that only here and there has this species of lice acquired the ability to use *P. major*, have already been pointed out in the historical discussion. Of course it is very probable that owing to the adaptability of *Aphis sorbi* and the abundance of *Plantago major*, the insect may eventually use either summer host plant without any marked preference as shown at present.

Ross's statement that this aphid can maintain itself thruout the season on apple is very important. Unfortunately, his statement is not supported either by the work of Baker and Turner (1916 b) or by that of the writer, tho Brittain (1915 b and 1916) records experiments in which he carried the species thru the summer on apple in Nova Scotia. This important phase in the life cycle of this species needs more investigation, for should the species become able to thrive on apple thruout the season it might become a pest of the first magnitude.

*The summer forms*

The spring migrants, after settling down on the plantain, begin producing living young within two or three days. All of their immediate descendants are wingless viviparous females. The young congregate about their mothers and are commonly found on the underside of the lower leaves, at the base of young, tender leaves, or on the developing

flower stalks. The young grow very rapidly, and under favorable conditions become mature within from ten to fifteen days. Thruout the summer months breeding is continuous and generation follows generation with considerable rapidity. During the summer of 1916 at least six generations matured on the plantain. By the first week in August of that year the fourth generation was mature and ready to produce young. Then there came very dry, hot weather, which continued until well into September. During this time the lice were rather inactive, failed to grow rapidly, and died off in large numbers. Only on the lower leaves and at the base of the flower and leaf stalks did the aphids survive, and it was almost impossible to follow closely the number of generations.

During the summer of 1917 a more detailed study was made of the reproductive capacity of the summer generations on plantain. Starting with the spring migrants from the apple, continuous rearing experiments were conducted thruout the season. In 1916 the rearing experiments were conducted in large cages, in each of which several narrow-leaved plantains were growing under natural conditions (Plate IX). In this way enormous numbers of the young were obtained, considerable crowding occurred, and, as later noted, winged forms appeared in several generations. In 1917 the rearing work was all done on young narrow- and broad-leaved plantains growing in small pots in an outdoor insectary. By this method close observation could be made on the individual reproductive capacity, and, tho many hundreds of individuals were reared, only one winged form appeared on the plantain. This occurred in the third generation on plantain, counting the winged as the first.

In Reproduction Chart II and figure 120 is presented a rather interesting study of longevity and reproductive capacity of the spring and fall migrants, as well as the true summer forms, on their preferred host plant (*Plantago lanceolata*). It will be noted at once that the spring migrant shows a shorter longevity and a remarkable reduction in reproductive capacity as compared with the spring forms on the apple. The succeeding wingless generations are more productive than the winged migrants, the productive period is much longer, and the longevity is greatly increased; as compared with the forms on the apple, the longevity on the average is greater and the productive period is longer, whereas the reproductive

capacity is greatly lessened. In the case of the summer forms on plantain, no attempt was made to determine the daily reproductive capacity, the rearing cages being examined only as recorded in the chart. However, it will be observed that the daily average, which is very low as compared with the forms on apple, is fairly well distributed over a long reproductive period. This is not the case with the spring and fall winged migrants.

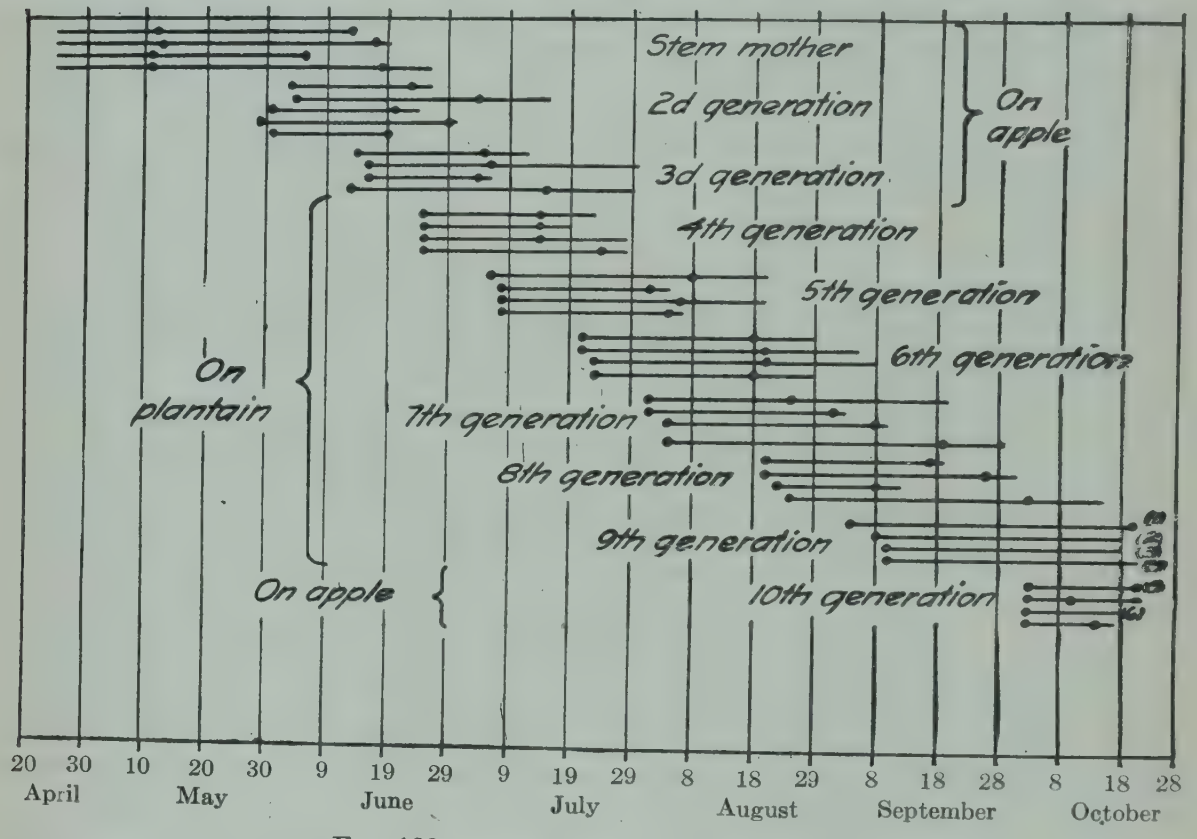


FIG. 120. GENERATIONS OF APHIS SORBI

The part of the line between the round dots represents the productive period; the remainder of the line represents the period of life after production ceased. The fourth generation all migrated to the plantain, and the tenth returned to the apple

(1) Died November 5; (2) died October 29; (3) ceased reproducing November 5, died November 16; (4) died November 4; (5) died October 21; (6) ceased reproducing November 5, died November 16

In these cases the reproductive period is reduced, whereas a marked reproductive activity occurs within the first few days after maturity is reached and the new host plant is occupied. The spring migrant gave an average daily production of 5.4 for five individuals during the first two days, followed by a daily production of only 1.4 during the next nine days. The fall migrant gave an average daily production of 3.2 for five individuals during the first three days, followed by only 0.34 during the next seven days, when reproductive activity practically ceased.

The reproductive activities of the spring and the fall migrants are undoubtedly due to the same factors, and are in marked contrast to those of the summer and spring forms. With the latter the rate of reproduction usually is low at first, gradually reaches its maximum, and then as gradually declines. The reproductive activities of the migrants can be explained, in all probability, in the following manner: They do not leave their host plants until a few days after reaching maturity, so that the reproductive organs are extremely active on reaching the new host plant. In order to avoid destruction by many agencies, such as climatic conditions, predatory enemies, or the like, it would seem essential that the greatest possible deposition of young should occur as soon as possible after the new host plant is found. So much of the vitality of these forms has been used in the production of wings and in the search for the new host plant, that a high reproductive capacity would seem physiologically impossible.

The summer generations consist very largely of wingless viviparous females. In 1916 winged forms appeared in the third, the fourth, and possibly the fifth generation, counting the descendants of the spring migrants as the first generation on plantain. In the third and fourth generations winged forms appeared in considerable numbers; the writer made no attempt, however, to determine the relative proportions of winged and wingless forms. This is in rather marked contrast to the results of Baker and Turner (1916 b), who record having observed but six winged forms thruout a summer's rearing work.[22] The winged forms developing in the large rearing cages were very active and flew about with great ease. Unfortunately the writer was unable to do much work with these forms, tho they reproduced normally and appeared well able to distribute the species during the summer. Whether these forms can return to the apple and breed there was not determined; the probability of such a condition has already been discussed (page 741).

Baker and Turner (1916 b) conclude that the summer winged forms are produced in such relatively small numbers that they are of no particular importance in the life history of the species. The writer cannot accept such a conclusion founded upon a single season's rearing work, particularly as different results were obtained at Ithaca. Furthermore, the large

[22] In the writer's rearing experiments of 1917, results similar to those of Baker and Turner were obtained. However, the writer does not consider such results as normal.

number of natural enemies which this aphid encounters on the plantain seems to necessitate a high productive capacity, which the species possesses, and also ability to spread to more distant host plants.

*Habits of the summer forms*

The summer forms on the plantain are much more active and agile than those occurring on the apple. Their legs are relatively longer when compared to the length of the body, and they can run with great rapidity. If an infested leaf or flower stalk is jarred or moved, the aphids at once remove their beaks and scurry rapidly for cover or drop to the ground. On the ground they hasten away and can travel considerable distances. In several rearing cages the aphids became so abundant that they caused the death of large plants. In such cases they climbed about the inside of the cage in immense numbers, endeavoring to find any possible exit. When the cages were opened they ran out very rapidly, and if they escaped their natural enemies it was not long before another plant was found. Undoubtedly this is the common way in which the species spreads from plantain to plantain during the summer.

*Description of stages*

*Summer wingless viviparous female, adult.*— Length 1.4–1.6 mm.; width 0.8 mm.; cornicles 0.4 mm. long.

The general color is light lemon yellow, usually with a faint reddish tinge on the dorsum of the metathoracic segment, and reddish yellow to reddish around and between the cornicles; in older specimens the color may become almost brown; the distal parts of the antennae, and the cornicles, the eyes, and the tarsi, are black. The antennae (fig. 114, D, page 705) are 6-segmented, slender, long, reaching beyond the tips of the cornicles. The segments are imbricated, and lack sensoria except an apical one on Segment V and the usual group at the distal end of the basal part of Segment VI. The length of the segments is as follows: Segment III, 0.4 mm.; Segment IV, 0.32 mm.; Segment V, 0.24 mm.; Segment VI, 0.12 + 0.36 mm. The head has a faint median tubercle; the dorsal tubercles are absent; the abdomen and the thorax lack the lateral and dorsal tubercles so prominent in the forms on apple. The cornicles are cylindrical, slender, slightly curved, and distinctly flanged (fig. 115, D,

page 706). The legs are long and slender, giving the wingless summer forms a slender and active appearance.

The above description is based largely on the adult wingless females of the first, second, and third generations on plantain, counting the descendants of winged migrants as the first generation. Tho there is considerable variation in size, and frequently in color markings, of the wingless females of each generation, yet these are not of sufficient importance to warrant special description.

*Summer winged viviparous female.*— This form appeared in considerable numbers in some of the writer's large rearing cages, which is in marked contrast to the results of Baker and Turner (1916 b). Descriptions of the fourth and the fifth (adult) instar follow.

Fourth instar.— The general color is bright red, except for the legs, the cornicles, the antennae, the head, and the wing pads; the head, the legs, the cornicles, and the basal half of the antennae are yellow; the apical half of the antennae, and the eyes, are black; the basal part of the wing pads is yellow, the tips brown to black; the cornicles are slightly dusky at their tips.

Fifth instar, adult.— Length 1.6 mm.; wing expanse 5 mm.

The winged summer female is almost identical to the spring migrant in color characters. The quadrate black area on the dorsum of the abdomen may be lacking in some cases, while in many others it is not so large as in the spring migrant. Otherwise there are no distinguishing characteristics.

### *Autumn forms*

Late in the autumn there appear special winged forms which return to the apple. These are known as the autumn, or fall, migrants. They consist of winged viviparous females and winged males. They begin to appear in the region of Ithaca late in September, the winged females developing first. There is no general migration in the true sense of that term, as these winged forms continue to return to the apple thruout the latter part of September and the whole of October, reaching their maximum, however, about the middle of the latter month. Stragglers also appear in November. The males begin appearing somewhat later and continue migrating to the apple well into November.

Both the winged males and the winged females are active, capable of flying very considerable distances and of walking or running with considerable agility. In the rearing cages they would fly actively about, being strongly attracted to the sunny side, or would walk over the fine wire mesh or cheesecloth. When liberated they flew away with a vigorous, direct flight.

*The winged female*

The females on reaching the apple usually seek out the underside of the leaves. Here they secure nourishment and deposit their young — the wingless oviparous females. They do not produce large numbers of young, nor do they deposit them in any one place, but seem to prefer to migrate from leaf to leaf depositing but a few young at a time.

The early instars of this form are identical with those of the spring migrant in practically every detail, and therefore it seems unnecessary to repeat the details here.

*The mature winged female, fall migrant* (Plate XXV).— Length 1.7–2 mm.; wing expanse 6 mm.

The autumn migrant is somewhat larger and more robust than the spring migrant. In color markings it does not vary to any extent, and it is only necessary to refer the reader to the description of the winged female of the third generation on apple. These winged forms, however, are frequently darker than the spring forms, appearing almost black, and agreeing very closely with the description given by Fitch (1855 a).

The antennae are 6-jointed and black. The third segment bears about 60 sensoria, the fourth about 30, the fifth from 6 to 12, and the sixth the usual group. The length of the segments is as follows: Segment III, 0.6–0.72 mm.; Segment IV, 0.4–0.5 mm.; Segment V, 0.25–0.32 mm.; Segment VI, 0.12–0.15 mm. + 0.6–0.7 mm. The head lacks the dorsal tubercles present in the spring migrant; very small lateral tubercles are present on the prothorax and on the abdominal segments; the last two abdominal segments are without dorsal tubercles. The cornicles are cylindrical, slightly curved, and distinctly flanged at their tips (fig. 115, E, page 706).

*The male*

The males are not so numerous as the females and usually appear later in the season. They are not so heavy-bodied and are more active.

In general structural details and color markings they do not differ from the female fall migrants, and no further description is needed.

The males on reaching the apple seek out the descendants of the female fall migrants and mate with them if they are mature. A single male mates indiscriminately with as many of the oviparous females as he can find.

*The oviparous female*

The immediate descendants of the female autumn migrants are known as the oviparous females. They are rather inactive, are smaller than the ordinary apterous summer forms, and are wingless. They are found on the underside of the apple leaves, but the writer has never found them causing a curling of the foliage similar to that caused by the spring forms. This form requires from twenty to thirty days to reach maturity, the nymphal stages varying greatly in length owing to the changing temperature conditions.

The mature oviparous female (Plate XXVI) is from 1.2 to 1.5 mm. in length. The general color is lemon yellow, with a faint greenish tinge near the margins of the body; around and between the cornicles is a rusty-red reticulated area, which is very characteristic; the head is grayish and the eyes are black. The cornicles are cylindrical and are distinctly flanged at their distal ends. The cauda is short and conical. The antennae are long. Sensoria are lacking, except a distal one on Segment V and the usual group at the base of the terminal filament of Segment VI (fig. 118, B, page 715). The length of the segments is as follows: Segment III, 0.16–0.2 mm.; Segment IV, 0.12–0.16 mm.; Segment V, 0.1–1.2 mm.; Segment VI, 0.32–0.34 mm. Lateral and dorsal tubercles are not present on the abdominal segment. Numerous sensoria are present on the hind tibiae (fig. 119, C, page 716).

*Oviposition.*— The mature oviparous females migrate to the smaller twigs and branches. There mating usually takes place, and the eggs are deposited around the base of buds, under small pieces of bark, or in any sheltered position. The writer has not been able to determine the number of eggs laid by many females, but in the few experiments conducted from four to six eggs were laid. This agrees with the results of Baker and Turner (1916 b), who record an average egg production of 6.3 for each female.

The egg is oval in form, and is slightly flattened on the side next the bark. The length is from 0.48 to 0.56 mm. The color is identical with that of the egg of *Aphis pomi*.

## THE APPLE-BUD APHIS, OR OAT APHIS

(*Aphis avenae* Fabricius)

The apple-bud aphis has been present in orchards in the eastern United States since the early part of the past century. It has been confused constantly with the two preceding species, *Aphis pomi* De G. and *A. sorbi* Kalt., and in many cases it is difficult if not impossible to determine to which species a writer is referring. It is not purposed in this article to present a detailed historical account of this species, inasmuch as this plant louse is a more serious pest of its summer host plants than of apple. However, it may be well to summarize briefly the synonymy of the species as it occurs in literature. This, according to the writer's views, is as follows:

1794 *Aphis avenae* Fabricius, Ent. Syst. **4** : 214.
1851 *Aphis malæ* Fitch, Cat. Ins. Cab. Nat. Hist., p. 65.
1855 *Aphis mali* (in part) Fitch, Trans. N. Y. Agr. Soc. **14** : 753.
1886 *Aphis annuæ* Oestlund, Geol. and Nat. Hist. Surv. Minn., Ann. Rept. **14** : 43.
1887 *Aphis annuæ* Oestlund, Geol. and Nat. Hist. Survey Minn., Bul. 4 : 66.
1902 *Aphis fitchii* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. **13** : 137.
1904 *Siphocoryne avenæ* Pergande, U. S. Div. Ent., Bul. 44 : 5.
1917 *Aphis prunifoliæ* Baker, Science (n. s.) **46** : 410–411.

### NATURAL HISTORY

The bionomics of this plant louse have been studied by a number of writers. The following account deals only with its life history and habits in relation to the apple, its primary host plant.

The eggs of *Aphis avenae*, like those of the two species already discussed, are laid in the autumn on apple, and at Ithaca hibernation takes place in this stage tho the writer has found the species hibernating as wingless viviparous females about the base of its summer food plants. Whether it can succeed in living thru northern winters and continuing its activities in the spring has not been accurately determined.

The eggs begin hatching in the spring from a week to ten days earlier than those of the green apple aphis or the rosy apple aphis. In the past three years the first eggs hatched on April 19 (1916), April 17 (1917),

and April 15 (1918). Hatching continues over a considerable period, usually about ten days if the weather is favorable. The stem mothers become mature during the last few days of April and the first week of May.

In some years this plant louse is extremely abundant and may be found in great swarms on the opening apple buds. Since the stem mothers hatch at the time of the swelling of these buds, the lice may be found congregated at the very tips seeking entrance even before the tips show green. As the buds unfold, the lice feed indiscriminately on the tender foliage but do not cause any marked curling of the leaves. Altho the lice were extremely abundant in 1915 they did scarcely any damage. Undoubtedly they reduced the vitality of the foliage to some extent, but not enough to be noticeable as compared with the injury caused by *Aphis pomi* and *A. sorbi.*

### *The stem mother*

In the species *Aphis avenae* the stem mothers reach maturity in about two weeks after hatching from the eggs. They feed almost exclusively on the opening foliage but do not cause any curling. They never attack the tender twigs, and have never been observed feeding on the water sprouts as is so common with the green apple aphis. The stem mothers become mature early in May. Altho a large number were reared in 1915, only a few were successfully carried thru the productive period. Deposition of young usually begins within from twenty-four to thirty-six hours after the last molt. In the individuals carried thru a normal life, the productive period was 30 days, the total production of young averaged 75, and the average daily production was 2.58. The total length of life was 44 days.

*Description of stages*

*First instar* (Plate XVIII).— The young nymph is dark green in color, with slightly lighter green down the middle of the dorsum; the head bears two black quadrangular areas on the dorsal surface, separated along the middle by a dark green line; the antennae, the legs, and the cornicles are almost black. The antennae are short, reaching to about the end of the thorax (fig. 111, c, page 684). The cornicles are very short, forming scarcely more than prominent disks (fig. 111, c). These last two characters readily separate this nymph from those of the other two species.

*Second instar.*— The color of the second instar is yellowish green, with the characteristic bright green diamond-shaped areas beginning to show on the dorsal surface of the abdomen; these, however, do not yet form a marked continuous line as appears in the later instars; the head is dark green; the legs and the cornicles are brown to almost black. The cornicles are still very short.

*Third instar.*— The third instar differs little from the second in color markings. The bright green diamond-shaped areas on the dorsum of the abdomen now form a continuous line, distinctly differentiating this species from the other two.

*Fourth instar.*— This instar is practically identical with the mature stem mother and does not require a separate description.

*Mature stem mother* (Plate XXI).— Length 2–2.15 mm.; width 1.2–1.3 mm.

The general color is yellowish green, the sides darker green; there is a broad median dorsal green stripe; at each segmental suture this stripe broadens out laterally, giving a somewhat diamond-shaped appearance to the green area of each segment; the distal ends of the antennae and the tibiae, the tips of the cornicles, and the tarsi, are dusky to black; around the base of the cornicles and between them there is frequently a reddish yellow area; the head is concolorous with the body; the eyes are black. The cornicles are cylindrical, slightly constricted at base and apex, with flaring tips (fig. 113, C, page 702). The antennae (fig. 112, B, page 685) are 5-jointed. The length of the antennal segments is as follows: Segment III, 0.32 mm.; Segment IV, 0.09 mm.; Segment V, 0.24 mm.

### *The second generation*

The young nymphs of the second generation feed almost exclusively on the foliage; rarely have they been found on the developing fruit. At Ithaca the majority of this generation acquire wings and migrate to the summer host plants. A small proportion are wingless viviparous females and continue to produce young on the apple.

*Description of stages*

*First instar.*— The young nymph is yellowish green in color, with the mid-dorsal green stripe plainly visible; the tips of the antennae, the

distal ends of the tibiae, and the tarsi, are dusky; the cornicles are yellowish green, dusky to black at their tips. The cornicles are similar in shape to those of the first instar of the preceding generation.

*Later instars.*— The remaining instars are similar in all essential markings to the first and require no special description.

*Mature viviparous female.*— The general color of the mature female is light yellowish green, with a distinct mid-dorsal green stripe as in the stem mothers; the distal half of the antennae is dusky; the eyes are black; the basal half of the cornicles is yellowish green, the tips are dusky. The cornicles are cylindrical, slightly constricted at base and tip, the distal ends flaring. On the sides of the anterior abdominal segments a whitish pulverulence is often present.

### *The third generation*

Normally there are comparatively few individuals of the third generation. All of them become winged and migrate to their summer host plants. The habits and characteristics of this generation are similar to the preceding and need no further discussion.

*Description of stages*

The nymphal stages differ in no essential from those of the preceding wingless generation. The developing wing pads readily distinguish the forms that are to acquire wings, but their color markings are essentially the same.

*Winged viviparous female, spring migrant* (Plate XXVII).— The winged female measures from 1.6 to 2 mm. long. The general color is dark green; the head, the antennae, the pronotum, and the thoracic lobes are dark olive-brown to black; the pronotum is margined in front and behind with yellowish green to dark green; on each side of the abdomen are three distinct black spots; at the base of the abdomen is a prominent transverse black stripe; the cornicles are brown to black, with a dark, almost black, area around the base; the legs are yellowish green except the tips of the femora and the tibiae, and the tarsi, which are dusky to black. The cornicles are cylindrical, constricted at the base and before the tips, which are flared somewhat irregularly (fig. 115, B, page 706). The antennae are shorter than the body and bear many characteristic sensoria

(fig. 114, B, page 705). The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.3 mm., sensoria 8–10; Segment IV, 0.19 mm., sensoria 6–8; Segment V, 0.16 mm., sensoria 1; Segment VI, 0.1 + 0.35 mm., sensoria the usual group.

### *Summer life history*

At Ithaca only three generations are normally produced on the apple. The winged migrants have practically all left for their summer host plants early in June, a few stragglers being found up to the end of that month. These summer host plants consist of a large number of grasses and cultivated grains; a full list is given by Davis.[23]

During the summer a large number of wingless and winged generations are produced. Late in the autumn, with the approach of cold weather, a winged migrating form appears, and this returns to the apple. At Ithaca these fall migrants begin to appear on apple and hawthorn about the last week in September. From that time to about the last week in October they continue to appear in increasing numbers, often in swarms. Their maximum flights probably occur about the last week in October. At that time they alight in great numbers on almost any object. They seem to be partial to white objects, and on examining white clothing hung out to dry it is very common to find on it great numbers of these lice.

### *The fall migrant*

The fall migrant of *Aphis avenae* is more active than that of *A. sorbi*, and normally is found in much greater abundance. It continues to appear later in the season and settles in great numbers on apple and hawthorn species. The first migrants are all winged viviparous females, and as soon as they reach their food plants they settle on the underside of the leaves and feed. The males begin to appear about a week to ten days after the first females. Deposition of young begins usually within a day or two, and small colonies are soon found settling down close around the winged forms. Several such colonies can be readily found on a single leaf. As the season advances these colonies become more and more abundant.

[23] Davis, J. J. The oat aphis. U. S. Dept. Agr. Bul. 112:1–16. 1914.

An interesting feature of this situation is the great number of the young viviparous females that undoubtedly perish thru the falling of the leaves. On a hawthorn near the Cornell University campus, great numbers of migrants had settled in the fall of 1914. The oviparous females began oviposition on October 20. They probably reached their maximum numbers on the foliage about October 28, on which day there was a severe frost. By the evening of the 29th practically all the leaves had fallen, destroying thousands of the still immature oviparous females. Similar occurrences took place on neighboring apple trees, tho the falling of the leaves was not so marked. As a consequence comparatively few eggs were laid. This undoubtedly happens every year, particularly when there are early frosts followed by high winds.

*Description of fall migrants*

*Winged viviparous female* (Plate XXVIII).— The winged viviparous female is from 1.6 to 2 mm. long. The head, the pronotum, and the thoracic lobes are black, the last-named shining; the pronotum may be margined in front and behind with a narrow band of dark green, but these bands do not show clearly in many specimens; the antennae, the eyes, the distal lobes of femora and tibiae, and the tarsi, are black; the abdomen is green, with from three to four black spots on each side in front of the cornicles and a narrow black band at the base of the abdomen; caudad of the cornicles are a dark area on each side and one or two narrow dusky to black bands across the tip of the abdomen; the cauda is brownish or greenish brown; the anal plate is black; the legs, except as noted above, are yellowish green; the cornicles are brown to pale greenish brown. The cornicles are cylindrical, constricted somewhat at the base and before the apex, which is flared somewhat irregularly (fig. 115, F, page 706). The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.32 mm., sensoria 12–16; Segment IV, 0.16 mm., sensoria 4–6; Segment V, 0.18 mm., sensoria 2–4; Segment VI, 0.8 + 0.46 mm., sensoria the usual group.

*Winged male.*— The winged male is from 1 to 1.5 mm. long. The general color markings are similar to those of the female, except that the abdomen is usually yellowish brown marked with considerable black in front of and between the cornicles; the antennae are black and about as long as the body; the cornicles are dark brown to black, and are similar in shape

to those of the winged female. The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.24 mm., sensoria 14; Segment IV, 0.12 mm., sensoria 3; Segment V, 0.12 mm., sensoria 2; Segment VI, 0.8 + 0.35 mm., sensoria the usual group.

*Oviparous female* (Plate XXIX).— The oviparous female is from 1 to 1.3 mm. long. It is distinctly elongate-oval in outline. The general color is yellowish green, shading more or less to brownish green or in some cases to almost green; the antennae and the legs are somewhat brownish; the cornicles are short, brown to almost black; frequently there is an orange-colored or reddish yellow area around the base of the cornicles, but this may be absent in older specimens. The cornicles are cylindrical, constricted before the apex, which is markedly flared (fig. 117, B, page 714). The hind tibiae are somewhat enlarged and flattened, and bear from 29 to 32 sensoria (fig. 119, B, page 716). The cauda is distinct, tapering, bordered with three pairs of hairs. The length of the antennal segments (fig. 118, C, page 715) and the number of sensoria are as follows: Segment III, 0.18 mm., sensoria 0; Segment IV, 0.094 mm., sensoria 1; Segment V, 0.053 + 0.22 mm., sensoria the usual group.

The egg is oval in form, and is slightly flattened on the side next the bark. Its length is from 0.48 to 0.56 mm. In color it is identical with the egg of *Aphis pomi*.

## EFFECTS OF ATTACKS OF PLANT LICE ON THE APPLE TREE AND ITS FRUIT

### THE GREEN APPLE APHIS

The work of the species *Aphis pomi* is very characteristic and is easily distinguished from that of the other two species, *A. sorbi* and *A. avenae*. As soon as the apple buds begin to open, the lice congregate on the tips of the leaves and soon penetrate deep into the unfolding buds, inserting their beaks and sucking out the juices. They particularly attack the leaves and the flower stalks, and as soon as the tender shoots (Plate VII), especially the water shoots, form, they crowd in dense masses on these, frequently killing them outright. In these dense crowds of lice on the water shoots *Aphis avenae* also may be present, at least early in May, but *A. sorbi* is not present.

*Aphis pomi* is also a leaf-attacking form, and is generally found on the under surface of the leaf crowded about the midrib and the lateral veins.

When abundant the lice cause the leaves to curl, but not so markedly as does *Aphis sorbi*. The leaves never form a close, tight curl, as is so common with the latter species, but the curl is more open, the tip of the leaf rarely doing more than touching the base. Later in the summer, usually in late July and August when there is sometimes a severe outbreak of *Aphis pomi*, the curling of the foliage may be more marked (Plate X). This is particularly true as the lice congregate on the rapidly growing twigs, stunting them and causing all the foliage to curl badly and in many cases to turn black and die. In young orchards serious damage may be done by the dwarfing and stunting of the rapidly growing shoots.

As the fruit begins to set, it may be attacked by countless swarms of these green lice, which congregate about the calyx end, on the stalk, and around the base, of the apple. The action of these numerous pumps at work sucking out the juices of the apples causes them to become elongated, puckered, and distorted, with many characteristic creases on the surface (Plates X–XII). Such badly injured fruits may drop in great numbers in June, considerably reducing the expected crop; or they may remain on the trees and become hard and knotty, growing to a slight extent and usually forming clusters — the so-called "cluster fruits" (Plate XII). The apple crop has been seriously injured in this way in many sections in the past few years.

Where this plant louse is abundant it greatly reduces the vitality of the trees, prevents the formation of fruit buds, distorts and deforms the foliage, often kills many of the succulent shoots, and causes knotty and gnarled apples. Recent experiments have shown that it also seems to be an active agent in the transmission of fire blight, one of the worst diseases in nurseries and in apple and pear orchards.

### THE ROSY APPLE APHIS

The rosy apple aphis (*Aphis sorbi*) hatches during the same period as the green apple aphis. It first attacks the opening buds, appearing to be particularly attracted to the flower buds (Plate XIII). In these the stem mothers congregate, and their progeny soon swarm over the developing leaves, the opening flowers, and the flower stalks. When the lice are abundant they may prevent the flowers from opening properly, and cause the flower stalks to weaken and oftentimes to bend to one side. The

leaves surrounding the cluster are severely curled, distorted, and usually blackened by the growth of a sooty fungus in the honeydew. When the infestation is very severe, few if any apples may set in such a cluster, or, if they do set, they are likely to drop early.

Not only does the rosy apple aphis attack the flower clusters, but in severe infestations it may spread over the entire foliage, tho generally most of the injury is low down in the tree around the outer margin. The leaves become badly curled, forming tight rolls within which myriads of lice are at work and from which migrations to the surrounding foliage constantly occur (Plates XIII and XIV).

This species probably does the severest damage to the fruit of any of the three species discussed in this paper. Parrott (1916 and 1917) performed some interesting experiments on the inhibition of growth of the fruit due to the attacks of the three species. He found that the greatest inhibition of growth, in both axial and transverse diameters of the fruit, was due to the attacks of the rosy aphis. Fruits that have been injured are usually elongate, puckered at the calyx end, and somewhat distorted (Plates XV–XVII). If not too badly injured, such fruits cling to the tree, growing but slightly and giving the so-called "cluster apples" at picking time. These cluster apples consist usually of from four to seven apples on a spur, which are small, distorted, and knotty. In a badly infested orchard, cluster apples may form the majority of the fruit at picking time.

### THE APPLE-BUD APHIS

Since the species *Aphis avenae* hatches from a week to ten days earlier than the other two species, it is the first one found on the bursting buds. When abundant, as is frequently the case, it may almost completely cover the buds. As the buds open, the young lice swarm over the leaves but never cause them to curl. Since in this vicinity practically all of the descendants of the stem mothers become winged and leave for their summer host plants, they do scarcely any serious damage to either the foliage, the fruit, or the developing shoots.

### THE APHIS SITUATION DURING THE LAST OF JUNE EACH YEAR

Before closing the discussion of injury to the apple, a summary of the situation during the latter part of June may be worthy of consideration.

At this period the aphis situation is usually a serious one for the orchardist, especially if he has not sprayed to control the lice and if the predacious and parasitic enemies of plant lice are not present in very considerable numbers. The factors determining the numbers and activities of the enemies of plant lice are many and are extremely complicated. No experimental work has been done on this phase of the problem, and up to this time only general statements based on field observations occur in the literature. With adequate facilities, two factors — temperature and moisture — might be studied. It is almost certain that these two factors are the controlling ones, but how they act has not been determined.

The reproductive capacity tables show that during the latter half of June the stem mothers probably cease reproducing and most of them die. The second and third generations are reproducing at their maximum, and the fourth generation of *Aphis pomi* will reach its maximum about the last days of June. It will thus be seen that if the parasitic and predacious enemies have not kept pace with their hosts, the severest injury may occur during the latter half of June. This is what occurs in an aphis year, and the reason for it can readily be seen by consulting the reproductive capacity tables. During the remainder of the summer, from July 1, the numbers of plant lice generally decrease, and this despite the fact that young of *Aphis pomi* are being produced in countless millions. The season has now become warm, a condition apparently most favorable for parasitic and predacious enemies, and these are able to gain the upper hand.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

# THE CRANE-FLIES OF NEW YORK

## PART I. DISTRIBUTION AND TAXONOMY OF THE ADULT FLIES

CHARLES PAUL ALEXANDER

ITHACA, NEW YORK
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## PART I. DISTRIBUTION AND TAXONOMY OF THE ADULT FLIES[1]

CHARLES PAUL ALEXANDER

The crane-fly fauna of New York State may be considered as representative of that of northeastern North America. For more than half a century New York has been one of the favorite collecting grounds for students of this neglected group of insects. The original plan of the present paper was to include only the species that are actually known to occur in this State. However, it should be understood and appreciated that in groups of insects which have been long ignored by almost all students of entomology, such as the group under consideration, it is still impossible to give the exact range of any particular species, and forms that seem to be confined to certain sections of the country upset all calculations by reappearing in distant regions which had been considered as far outside the range of the species. Thus it is possible that almost any species occurring in northeastern America may be found within the limits of this State, altho some species are now known only from localities so distant as to make it seem improbable that they may be found here also. For this reason the scope of the present paper has been extended to include the northeastern United States and eastern Canada — Labrador and Newfoundland, south to Virginia and Kentucky, west to Iowa, Minnesota, and Manitoba. It is believed that this area includes about all of the local probabilities, but there are undoubtedly new species yet to be discovered and lost species to be recognized.

The number of species of crane-flies that should occur in New York State is probably not less than three hundred, and this figure seems similarly applicable to many areas of equal extent and equal diversity of ecological conditions in the North Temperate Zone.

The student of this group of flies will find that there is still very much to be done in determining the exact seasonal and geographical distribution

[1] This study was conducted in the entomological laboratory of Cornell University, under the direction of Dr. James G. Needham, Dr. J. Chester Bradley, and Dr. O. A. Johannsen, to whom the writer is indebted for many helpful criticisms and suggestions.

of the species here included. Present knowledge of the biology and ecology of these species, and exact data on the duration of the different periods of the immature stages, are still very meager, and it is this field more than any other that offers the greatest opportunities for research.

The classification herein adopted is that of Osten Sacken, but it may be well to state that very many fundamental changes are to be expected when the immature stages are better known.

In the course of the author's studies on the local Tipulidae, it was necessary for him to visit and examine most of the important collections in the East. In some cases in which it was impracticable to visit the museums, specimens were lent by the authorities in charge. The writer wishes to express his gratitude to the persons who kindly assisted in this manner. Among the collections studied were those contained in the following institutions:

United States National Museum, Washington, D. C. This museum contains probably the largest collection of crane-flies in the New World, including the types of Coquillett and the Limnobiinae described by Doane, as well as much of the material determined by the author. The collection was examined on several occasions thru the kindness of the late Mr. Frederick Knab, custodian of the Diptera.

United States Biological Survey, Washington, D. C. The collections here, examined thru the kindness of Mr. W. L. McAtee, are extensive, and are particularly rich in local forms and in material from the Pribilof Islands.

Museum of Comparative Zoology, Cambridge, Massachusetts. These collections, examined on several occasions thru the kindness of the Director, Mr. Samuel Henshaw, include the types of Osten Sacken and Loew and are of the greatest importance on that account. The material is in a fine state of preservation because of the constant care given to it.

Boston Society of Natural History, Boston, Massachusetts. These collections, examined thru the kindness of the Curator, Mr. Charles W. Johnson, are very fine, almost complete as far as the New England fauna is concerned, and of great value to the student. The type of *Chionea valga* Harris, as well as many of Say's species and the specimens determined by him, are to be found here.

Academy of Natural Sciences, Philadelphia, Pennsylvania. The material here includes the collections of the American Entomological Society. The collections were examined thru the kindness of Mr. E. T. Cresson, jr. They include the type of *Triogma exculpta* Osten Sacken, and cotypes of many of the other Sackenian species as well as a good representation of other forms.

American Museum of Natural History, New York City. This rather considerable collection, examined thru the kindness of Dr. F. E. Lutz, includes many of Williston's cotypes and is especially rich in Antillean and South American forms.

Museum of the Brooklyn Institute, Brooklyn, New York. This collection was examined thru the kindness of the custodian, Mr. Charles Shaeffer. It is a rather small local collection, but the specimens have been authoritatively determined by Johnson and they form a good nucleus for future work.

New York State Museum, Albany, New York. This is a good local collection, examined on several occasions thru the kindness of the State Entomologist, Dr. E. P. Felt, and the assistant entomologist, Mr. D. B. Young.

Cornell University, Ithaca, New York. This collection is under the direction of Dr. James G. Needham and Dr. J. Chester Bradley. It is a very complete collection, including many specimens taken in the seventies by Professor J. H. Comstock and the late Mr. H. H. Smith and determined by Osten Sacken. The type of *Rhabdomastix flava* is here.

Maine Agricultural Experiment Station, Orono, Maine. This is a very good local collection, made in large part by the author in 1913, under the employment of the Director, Dr. Charles D. Woods, and the Station Entomologist, Dr. Edith M. Patch.

Department of Entomology of North Carolina, Raleigh, North Carolina. This collection was examined thru the kindness of the State Entomologist, Mr. Franklin Sherman, and Mr. R. W. Leiby. It is a good collection of local material.

Ohio State University, Columbus, Ohio. This collection was examined thru the kindness of Professor James Hine, who collected the greater part of the material.

University of Minnesota, St. Paul, Minnesota. This is a good local collection, including most of the material mentioned in Washburn's *Diptera of Minnesota*. It was sent to the writer by Mr. Simon Marcovitch. Considerable additional material from the region of Lake Itasca was given to the writer for determination by the collector, Mr. Samuel A. Graham.

Washington State Agricultural College, Pullman, Washington. This collection is very important, as it contains many of the Tipulinae described by Doane. The writer was unable to visit the collection, but Dr. Axel L. Melander very kindly sent him the cotype specimens of three or four eastern species that were needed in the preparation of this paper.

Canadian National Museum, Ottawa, Ontario. This collection was sent to the writer for naming, thru the kindness of the Dominion Entomologist, Dr. C. Gordon Hewitt. It is a rather extensive collection, from most parts of the Dominion.

University of Toronto, Toronto, Ontario. This is a small collection, mostly taken by Dr. E. M. Walker and including the types of *Phalacrocera neoxena*. It contains also a few additional specimens collected by Dr. W. A. Clemens and including the type of *Tipula algonquin*.

New Brunswick Experiment Station, Fredericton, New Brunswick. This is a good local collection, taken by the Station Entomologist, Mr. John D. Tothill.

Nova Scotia Experiment Station, Truro, Nova Scotia. This is a very good local collection, taken by Dr. Robert Matheson. It is now in the collection at Cornell University.

In addition to the public collections listed above, there are in the United States a few private collections of great value, as follows:

The collection of Dr. W. G. Dietz, Hazleton, Pennsylvania. This is a very considerable collection of North American species, including the types of the species described by the owner.

The collection of Mr. C. W. Johnson, Boston, Massachusetts. This is an exceptionally fine collection, and includes the types of many of the species described by the owner.

The collection of Dr. J. G. Needham, Ithaca, New York. This is a good local collection, mounted in balsam. It includes the types of *Dicranomyia whartoni* and *Dolichopeza americana*.

The collection of Mr. M. C. Van Duzee, Buffalo, New York. This collection is very rich in local and Floridian species, and includes the type of *Geranomyia vanduzeei*.

The collection of the author, Urbana, Illinois. This includes a good representation of local forms and many extra-limital species. The types of many of the species described by the author are in this collection.

In addition to those named above, there have been examined several collections made by students in systematic entomology at Cornell University during the past few years. The more notable of these are the collections of Dr. W. T. M. Forbes, and Messrs. J. T. Lloyd, S. W. Frost, E. A. Richmond, W. C. Woods, and Hachiro Yuasa. The following very considerable collections, made in different parts of the country, have been of great value in determining the range of North American species:

The two Beutenmüller collections, one in the American Museum and the other in the collection of Dr. Dietz, from the Black Mountains, North Carolina.

The Nathan Banks collections, from the same locality and from northern Virginia.

The Karl P. Schmidt collection, made in Louisiana.

The J. Chester Bradley collections, made in Georgia, New York, and the West.

The R. C. Shannon collections, from the vicinity of Washington, D. C.

The Axel Olsson collections, from North Carolina and New York.

The H. H. Knight collections, from western New York.

The H. M. Parshley collections, from Maine and Massachusetts.

The Cordelia Stanwood collections, from Hancock County, Maine.

Collections made in the vicinity of Georgian Bay, Ontario, by Dr. W. A. Clemens in 1912, by Mrs. John D. Tothill in 1914, and especially by Mr. H. S. Parish in 1915.

The Bryant Newfoundland specimens in the collection of Mr. Johnson.

Material from near Washington, D. C., and from Maine, collected by Mr. W. L. McAtee.

The Ely (Connecticut) and Weidt (New Jersey) material in the collection of Dr. Dietz.

The extensive collections made in Bergen County, New Jersey, by Mr. M. D. Leonard.

Specimens collected by Oslar (Colorado), Munz (Colorado), and Woodgate (New Mexico), and other material in the collection of the author.

To all the above-mentioned persons the author expresses his sincere gratitude for the privilege of seeing these specimens and obtaining the records.

In addition to the collections that the writer has been able to visit, there are several others of high repute — the collection in the Carnegie Museum (Pittsburg, Pennsylvania), the private collection of Mr. Charles Dury (Cincinnati, Ohio), the collections of the Illinois State Laboratory of Natural History and the University of Michigan, and others —

which unquestionably will supply many new, chiefly local, records when their contents are made known.

## SYSTEMATIC POSITION OF THE SPECIES

The families that make up the insects known as crane-flies are four in number — the Tanyderidae, the Ptychopteridae, the Rhyphidae, and the Tipulidae. All but the last-named of these families are very limited in number of species, the total number of described forms being not far in excess of threescore. Crane-flies belong to the division Nematocera of the suborder Orthorrhapha. They are characterized by having six or more segments in the elongated antennae. The only families of flies with which crane-flies might be confused are the Bibionidae and the Dixidae.

Crane-flies are very often of large size. They are the largest of the Nematocera and are among the largest of all Diptera. The differences in size found in the family Tipulidae are very great, ranging from the giants of the family, *Ctenacroscelis praepotens*, *Tipula brobdinagia*, and others, down to such species as *Erioptera parva* and *Molophilus ursinus*, veritable pygmies. In the area considered in this paper, the largest species found are *Longurio testaceus* and *Tipula abdominalis*, and the smallest is *Molophilus ursinus*.

In appearance crane-flies may be described as mosquito-like and they are very often mistaken for mosquitoes, the larger species often causing great alarm. There are no crane-flies, however, that have the biting habits of the Culicidae. The legs of all crane-flies are long and slender, in some cases being exceedingly so, and this feature has given most of the common names that are applied to these insects — crane-flies, daddy longlegs, and the like. The wings are many-veined (polyneura), and in most species they possess a completely inclosed discal cell (*1st* $M_2$). In all Tipulidae and in the trichocerine Rhyphidae there are two anal veins, a character never possessed by the more specialized Nematocera. On the mesonotum there is a distinct, more or less transverse, V-shaped suture separating the prescutum from the scutum. In the Tanyderidae, the Ptychopteridae, and the Rhyphidae this suture is rather poorly defined. Ocelli are found only in the Rhyphidae. The large size, the inclosed discal cell, the presence of two anal veins, and the V-shaped suture, are sufficient to distinguish the local species of Tipulidae.

## ECONOMIC IMPORTANCE

Economically, crane-flies are found to play a relatively important rôle. The adult flies are entirely harmless, but the larvae of many species are destructive to various crops. In Europe the best-known of such species is *Tipula oleracea* Linn. In eastern North America the smoky crane-fly, *T. cunctans* Say (called *T. infuscata* Loew by Hyslop, 1910[2]), working principally on leguminous species, and *T. bicornis* Forbes working largely on grasses, often become serious pests; in the West the alfalfa crane-fly, *T. simplex* Doane (Essig, 1913), is often of exceedingly great importance, working on various legumes and grass species. Other species, as *T. derbyi* Doane and *T. aspidoptera* Alex., often do considerable local damage. In Japan, *T. longicauda* Mats. and a species that has been determined as *T. parva* Loew do very considerable damage to rice and sugar cane. It is to be noted that all these more destructive species belong to the tribe Tipulini, comprising the larger species of crane-flies, and the damage is done by the larvae's feeding on the roots and thus causing the death of the plants.

The species of Tanyptera live in logs or stumps that are fairly sound and free from decay. The larvae of some species of Rhipidia, Limnobia, Trichocera, and other genera, affect stored roots and tubers. The species of Ula and some species of Limnobia live in fungi (Boletus, Armillaria, Hypomyces, and others), and in some cases may be of economic importance in mushroom culture.

As an element of food for vertebrates, crane-flies occupy a prominent position. The records of Dr. Dallas Hanna and those of the Whitneys, in the possession of the United States Biological Survey, state that larvae representing an unknown species of Tipula are abundant everywhere thruout the summer season on St. Paul Island, of the Pribilof group in Bering Sea. These larvae are found around the roots of grasses and herbs, and especially under beds of moss, on the roots of which they feed, killing the moss over considerable areas. Under such a moss bed as many as twenty larvae to the square foot have been collected. The larvae must be of considerable ecological importance because of their food value to birds and foxes. Foxes will dig over large areas of moss beds to feed on them. Thruout the arctic regions the family Tipulidae

[2] Dates in parenthesis refer to *References cited*, page 959.

seems very abundant, both in number of species and in number of individuals, and the larvae are exceedingly numerous.

The Biological Survey has kept a very careful record of the food of birds and other vertebrates, based on the examination of stomach contents, and thru the kindness of Messrs. W. L. McAtee and E. R. Kalmbach the writer has obtained a record of the species known to feed on crane-flies. Over a hundred species of birds, representing almost all the bird families, have been found to feed on the adult flies. The more notable and general of these birds are sandpipers, flycatchers, vireos, swallows, wood warblers, and thrushes. The species feeding on the larvae consist for the most part of ducks, shore birds, and thrushes. Dr. Alice A. Noyes has found in the stomach of a Wilson's snipe twenty-three head capsules of a small Tipula (possibly *T. dejecta* Walker), showing the importance of the larvae as food at certain seasons. Similarly the food of toads (Bufo) and of frogs (Rana) often includes an abundance of larval and adult crane-flies (Needham, 1905).

The larvae of crane-flies are very tempting to many species of fishes. Certain of the larger larvae, such as those of *Tipula abdominalis* and *Eriocera spinosa*, furnish one of the best of baits for black bass and other game fish, being even more tempting in many cases than the better-known dobson (Corydalis). The skin of these larvae is very tough and leathery, hence their common name *leather-jacket*. The fishhook is run thru the body of the larva at about midlength, leaving the two ends wriggling. Studies made by Needham (1908:172–188) on the food of the bullhead, the sunfish, and the red-bellied minnow, showed that crane-flies were not eaten by these species, and the same is true of the brook trout in ponds (Needham, 1903a). But the habitat of the larvae is not in the haunts of these fishes. They live in the leaf drift caught in the eddies, in the mud and gravel at the sides and the bottom of the stream, and in similar situations which are not readily accessible to the fish. It seems probable that it is due to the fact that the larvae furnish such choice titbits, that they cannot exist in the same haunts with the fish. Some species, as those of Eriocera, live in the chutes of the Mississippi River, and they are the only crane-flies known from such a habitat. The remains of crane-flies, such as wings, legs, and heads, are often found in fish stomachs, these being from adult flies that have fallen into the water and been snapped up by the fish.

## DISTRIBUTION

### GEOLOGICAL DISTRIBUTION

The source of origin of the crane-flies is still largely problematical, but the preponderance of evidence now seems to indicate that they came from some neuropteroid ancestor far back in Mesozoic times. This is expressed by Needham (1908:221) as follows: "The suggestion has been made before by others, and I think it very possible, that some Panorpidlike neuropteroid mutant got its center of gravity hitched forward, its hind wings reduced, and started the dipterous line of evolution."

The first insects that can be definitely referred to the Tipulidae appeared rather suddenly in late Mesozoic times. They belong almost entirely to the subfamily Tipulinae, but the records are very scanty and for the most part unsatisfactory. The evidence that specimens of Tanyderidae, Ptychopteridae, or Limnobiinae occurred at that time is very doubtful. In the Tertiaries, however, the group was extraordinarily developed and it seems quite possible that the family reached its maximum of diversity in the Miocene period or a little later and is now a waning group. From the Oligocene period of British Columbia, Handlirsch (1910) has recorded a curious tanyderid under the name *Etoptychoptera*. The Florissant beds of Colorado were laid down in a lake that is supposed to be of the late Oligocene or the early Miocene age. There have been taken from these beds hundreds if not thousands of specimens, representing about seventy-five species, indicating the extreme richness of the crane-fly fauna during that age. On one slab of the deposit Scudder found a specimen of his *Dicranomyia inferna* which was partly overlain by a specimen of his *D. fontainei*, a condition very suggestive of the remarkable richness of this fauna. The abundance of species in the amber fauna, likewise of the Tertiaries, was indicated by Loew in 1850 and more recently elaborated by Meunier. The present knowledge of the Florissant fauna is due to the work of Scudder, Cockerell, and Wickham.

### GEOGRAPHICAL DISTRIBUTION

#### *A summary of the crane-fly fauna of the world*

The four families comprising the crane-flies are represented in almost every part of the world where life is possible. Apparently the range of the group is restricted only by great extremes of temperature.

The lesser oceanic islands (the Seychelles, the Fiji, the Hawaiian, and others) that have been at all studied are quite devoid of species of the subfamily Tipulinae, these species being of large size and often possessing considerable powers of flight; while the much smaller species in the Limnobiinae are often very numerous and may include a considerable range of species. Crane-flies in the arctic regions are very abundant and are represented by a few genera of Limnobiinae and many species of Tipula. Many of the latter have the wings atrophied so that they are incapable of flight. This condition is particularly true of forms along the coast or on wind-swept islands adjoining the mainland, and may be confined to the female sex alone or may be found in both sexes. It must be understood, however, that reduction of the wings is by no means confined to such environments or to the genus Tipula, since it occurs in almost all the major groups of crane-flies — in Limnobiini (Zalusa End.), Eriopterini (Platylimnobia Alex., Chionea Dalm.), Limnophilini (Zaluscodes Lamb, Alfredia Bezzi, *Limnophila aspidoptera* Coq.), Pediciini (*Tricyphona hannai* Alex.), and many others—and is found in many different parts of the world tho usually in arctic, oceanic, or mountainous situations. *Tipula besselsi* O. S., described from Polaris Bay, northern Greenland, is found above the 80th degree of north latitude and within a few hundred miles of the North Pole.

The four families of crane-flies include, respectively, the following numbers of genera, subgenera, and species:[3]

| | Genera | Subgenera | Species |
|---|---|---|---|
| TANYDERIDAE | 2 | ..... | 8 |
| PTYCHOPTERIDAE: | | | |
| Ptychopterinae | 1 | ..... | 12 |
| Bittacomorphinae | 2 | ..... | 4 |
| RHYPHIDAE: | | | |
| Trichocerinae | 2 | 2 | 22 |
| Rhyphinae | 3 | ..... | 26 |
| Mycetobiinae | 2 | ..... | 7 |
| TIPULIDAE: | | | |
| Limnobiinae: | | | |
| Limnobiini | 10 | 5 | 365 |
| Antochini | 15 | 1 | 160 |
| Eriopterini | 28 | 10 | 410 |
| Limnophilini | 16 | 10 | 290 |

[3] This table is dated June 1, 1916.

| | Genera | Subgenera | Species |
|---|---|---|---|
| TIPULIDAE (*continued*): | | | |
| Limnobiinae (*continued*): | | | |
| Hexatomini | 4 | ..... | 125 |
| Pediciini | 7 | 3 | 75 |
| Cylindrotominae | 5 | ..... | 16 |
| Tipulinae: | | | |
| Dolichopezini | 9 | 2 | 45 |
| Ctenophorini | 7 | ..... | 50 |
| Tipulini | 21 | 3 | 900 |
| Total | 134 | 36 | 2,515 |

The Tanyderidae have two living genera, one antipodal and the other (Protoplasa) with two Nearctic species.

The Ptychopteridae have three genera. One of these, Ptychoptera, is found in most parts of the world excepting Australasia, while the other two, Bittacomorpha and Bittacomorphella, are Nearctic.

The Rhyphidae have seven genera, arranged in three subfamilies. The species, with few exceptions, are from the North Temperate Zone.

Among the Tipulidae, the tribes Limnobiini, Antochini, Eriopterini, Limnophilini, Dolichopezini, Ctenophorini, and Tipulini are almost cosmopolitan. The tribe Hexatomini has the genus Hexatoma dominant in Europe, and the genus Eriocera cosmopolitan except for the Palaearctic and Australasian regions. The tribe Pediciini reaches its greatest development in the North Temperate Zone. The Cylindrotominae are Holarctic, with one genus (Stibadocera) occurring in the Oriental region.

### *Lists of the species of adjoining States and provinces*

The following lists of species are given to supplement the data on the New York fauna.

#### Maine

The data for Maine are based largely on the results obtained by the author from a study of the group during a period of fifteen weeks, under the direction of Dr. Charles D. Woods and Dr. Edith M. Patch. Very valuable collections in this State have been made by Mr. Charles W. Johnson, Miss Cordelia J. Stanwood, Dr. H. M. Parshley, Professor Herbert Osborn, Professor A. P. Morse, and others.

*Ptychoptera rufocincta* O. S.

*Bittacomorpha clavipes* (Fabr.)

*Bittacomorphella jonesi* (Johns.)

*Trichocera regelationis* (Linn.)

*Discobola argus* (Say)

*Dicranomyia badia* (Walk.)
*gladiator* O. S.
*globithorax* O. S.
*haeretica* O. S.
*halterata* O. S.
*immodesta* O. S.
*liberta* O. S.
*longipennis* (Schum.)
*morioides* O. S.
*pubipennis* O. S.
*pudica* O. S.
*rostrifera* O. S.
*simulans* (Walk.)

*Geranomyia diversa* O. S.
*rostrata* (Say)

*Limnobia cinctipes* Say
*hudsonica* O. S.
*immatura* O. S.
*indigena* O. S.
*parietina* O. S.
*solitaria* O. S.
*triocellata* O. S.
*tristigma* O. S.

*Rhipidia bryanti* Johns.
*maculata* Meig.

*Antocha saxicola* O. S.

*Elephantomyia westwoodi* O. S.

*Rhamphidia mainensis* Alex.

*Toxorhina muliebris* (O. S.)

*Cladura flavoferruginea* O. S.

*Cryptolabis paradoxa* O. S.

*Erioptera armata* O. S.
*armillaris* O. S.
*caloptera* Say
*chlorophylla* O. S.
*chrysocoma* O. S.
*needhami* Alex.
*septemtrionis* O. S.
*stigmatica* (O. S.)
*straminea* O. S.
*venusta* O. S.
*vespertina* O. S.

*Gnophomyia tristissima* O. S.

*Gonomyia florens* Alex.
*subcinerea* O. S.

*Molophilus comatus* (Doane)
*hirtipennis* (O. S.)
*pubipennis* (O. S.)

*Ormosia monticola* (O. S.)
*nigripila* (O. S.)
*nubila* (O. S.)
*pygmaea* (Alex.)
*rubella* (O. S.)

*Helobia hybrida* (Meig.)

*Adelphomyia americana* Alex.
*cayuga* Alex.
*minuta* Alex.

*Epiphragma fascipennis* (Say)

*Limnophila adusta* O. S.
*areolata* O. S.
*brevifurca* O. S.
*fasciolata* O. S.
*fuscovaria* O. S.
*inornata* O. S.
*lenta* O. S.
*luteipennis* O. S.
*macrocera* (Say)
*montana* O. S.
*munda* O. S.
*nigripleura* A. & L.
*novae-angliae* Alex.
*noveboracensis* Alex.
*osborni* Alex.
*quadrata* O. S.
*recondita* O. S.
*rufibasis* O. S.
*stanwoodae* Alex.
*tenuicornis* O. S.
*tenuipes* (Say)
*toxoneura* O. S.
*ultima* O. S.
*unica* O. S.

*Ula elegans* O. S.

*Ulomorpha pilosella* (O. S.)

*Eriocera longicornis* (Walk.)
*spinosa* (O. S.)

*Pedicia albivitta* Walk.

*Rhaphidolabis cayuga* Alex.
*flaveola* O. S.
*tenuipes* O. S.

*Tricyphona autumnalis* Alex.
*calcar* (O. S.)
*inconstans* (O. S.)
*katahdin* Alex.
*vernalis* (O. S.)

*Cylindrotoma americana* O. S.

*Liogma nodicornis* (O. S.)

*Phalacrocera tipulina* O. S.

*Dolichopeza americana* Needm.

*Oropeza dorsalis* Johns.
*obscura* Johns.
*sayi* Johns.
*venosa* Johns.

*Ctenophora apicata* O. S.

*Nephrotoma eucera* (Loew)
*ferruginea* (Fabr.)
*incurva* (Loew)
*lugens* (Loew)
*pedunculata* (Loew)
*punctum* (Loew)
*sodalis* (Loew)
*tenuis* (Loew)
*vittula* (Loew)
*xanthostigma* (Loew)

*Stygeropis fuscipennis* Loew

*Tipula abdominalis* (Say)
*algonquin* Alex.
*angulata* Loew
*angustipennis* Loew
*apicalis* Loew
*bella* Loew
*bicornis* Forbes
*caloptera* Loew
*cayuga* Alex.
*cunctans* Say
*fragilis* Loew
*hebes* Loew
*hermannia* Alex.
*longiventris* Loew
*macrolabis* Loew
*mainensis* Alex.
*nobilis* (Loew)
*oropezoides* Johns.
*parshleyi* Alex.
*penobscot* Alex.
*sayi* Alex.
*senega* Alex.
*serta* Loew
*strepens* Loew
*submaculata* Loew
*sulphurea* Doane
*tephrocephala* Loew
*trivittata* Say
*ultima* Alex.
*valida* Loew

**New Brunswick**

(The collections of the New Brunswick Experiment Station, made by Mr. John D. Tothill and others)

*Bittacomorpha clavipes* (Fabr.)

*Dicranomyia morioides* O. S.

*Geranomyia canadensis* (Westw.)

*Limnobia cinctipes* Say

*Erioptera armata* O. S.

*Limnophila adusta* O. S.
*imbecilla* O. S.
*inornata* O. S.
*quadrata* O. S.
*recondita* O. S.
*rufibasis* O. S.

*Eriocera longicornis* (Walk.)

*Liogma nodicornis* (O. S.)

*Oropeza sayi* Johns.
*venosa* Johns.

*Ctenophora apicata* O. S.

*Nephrotoma eucera* (Loew)
*ferruginea* (Fabr.)
*incurva* (Loew)
*lugens* (Loew)
*occipitalis* (Loew)
*pedunculata* (Loew)
*tenuis* (Loew)
*xanthostigma* (Loew)

*Tipula abdominalis* (Say)
*angulata* Loew
*angustipennis* Loew
*caloptera* Loew
*eluta* Loew
*hebes* Loew
*latipennis* Loew
*macrolabis* Loew
*parshleyi* Alex.

*Tipula strepens* Loew
*sulphurea* Doane
*tephrocephala* Loew
*ternaria* Loew
*Tipula trivittata* Say
*ultima* Alex.
*valida* Loew

**Nova Scotia**

(The collections of Dr. Robert Matheson, of Cornell University)

*Ptychoptera rufocincta* O. S.

*Bittacomorpha clavipes* (Fabr.)

*Trichocera bimacula* Walk.

*Dicranomyia haeretica* O. S.
*halterata* O. S.
*immodesta* O. S.
*liberta* O. S.

*Rhipidia maculata* Meig.

*Limnobia solitaria* O. S.
*triocellata* O. S.

*Discobola argus* (Say)

*Antocha saxicola* O. S.

*Elephantomyia westwoodi* O. S.

*Erioptera armata* O. S.
*armillaris* O. S.
*caloptera* Say
*chlorophylla* O. S.
*septemtrionis* O. S.

*Gonomyia mathesoni* Alex.
*sulphurella* O. S.

*Rhabdomastix flava* (Alex.)

*Cryptolabis paradoxa* O. S.

*Limnophila adusta* O. S.
*lenta* O. S.
*macrocera* (Say)
*noveboracensis* Alex.
*recondita* O. S.
*tenuicornis* O. S.
*toxoneura* O. S.

*Pedicia albivitta* Walk.
*contermina* Walk.

*Tricyphona inconstans* (O. S.)
*vernalis* (O. S.)

*Eriocera longicornis* (Walk.)
*spinosa* (O. S.)

*Liogma nodicornis* (O. S.)

*Tanyptera frontalis* (O. S.)

*Nephrotoma eucera* (Loew)
*ferruginea* (Fabr.)
*incurva* (Loew)
*lugens* (Loew)
*macrocera* (Say)
*pedunculata* (Loew)
*tenuis* (Loew)

*Tipula abdominalis* (Say)
*angustipennis* Loew
*apicalis* Loew
*bella* Loew
*caloptera* Loew
*cayuga* Alex.
*fragilis* Loew
*hebes* Loew
*hermannia* Alex.
*parshleyi* Alex.
*sayi* Alex.
*submaculata* Loew
*tephrocephala* Loew
*tricolor* Fabr.
*trivittata* Say
*ultima* Alex.
*valida* Loew

**Quebec**

The published list for Quebec (Winn and Beaulieu, 1915) has been revised, certain species being dropped, a few others added, and certain parts of the synonymy corrected. The record for *Dicranomyia distans* O. S., an Austral species ranging as far north as Washington, D. C., is evidently erroneous. The species of Trichocera and Tanyptera are

given as determined by C. W. Johnson. Our knowledge of the crane-flies of Quebec is due to the work of Beaulieu, Beaulne, Chagnon, Couper, Fyles, Winn, and others.

*Ptychoptera rufocincta* O. S.

*Bittacomorpha clavipes* (Fabr.)

*Trichocera maculipennis* (Fabr.)
*regelationis* (Linn.)

*Dicranomyia immodesta* O. S.
*liberta* O. S.
*longipennis* (Schum.)
*pudica* O. S.

*Limnobia cinctipes* Say
*indigena* O. S.
*solitaria* O. S.
*tristigma* O. S.

*Rhipidia maculata* Meig.

*Discobola argus* (Say)

*Antocha saxicola* O. S.

*Elephantomyia westwoodi* O. S.

*Rhamphidia flavipes* Macq.

*Chionea valga* Harr.

*Ormosia monticola* (O. S.)

*Erioptera armata* O. S.
*armillaris* O. S.
*caloptera* Say
*chlorophylla* O. S.
*chrysocoma* O. S.
*septemtrionis* O. S.
*venusta* O. S.
*vespertina* O. S.

*Molophilus pubipennis* (O. S.)

*Gonomyia subcinerea* O. S.

*Gnophomyia tristissima* O. S.

*Helobia hybrida* (Meig.)

*Epiphragma fascipennis* (Say)

*Limnophila adusta* O. S.
*areolata* O. S.
*brevifurca* O. S.
*contempta* O. S.
*fuscovaria* O. S.
*imbecilla* O. S.
*macrocera* (Say)
*montana* O. S.
*munda* O. S.
*quadrata* O. S.
*rufibasis* O. S.
*tenuipes* (Say)
*toxoneura* O. S.
*ultima* O. S.

*Pedicia albivitta* Walk.

*Tricyphona autumnalis* Alex.
*inconstans* (O. S.)

*Liogma nodicornis* (O. S.)

*Oropeza albipes* Johns.
*obscura* Johns.

*Ctenophora apicata* O. S.

*Tanyptera atrata* (Linn.)
*dorsalis* (Walk.)
*fumipennis* (O. S.)
*topazina* (O. S.)

*Nephrotoma eucera* (Loew)
*ferruginea* (Fabr.)
*incurva* (Loew)
*lineata* (Scop.)
*lugens* (Loew)
*occipitalis* (Loew)
*sodalis* (Loew)
*tenuis* (Loew)
*xanthostigma* (Loew)

*Stygeropis fuscipennis* Loew

*Tipula abdominalis* (Say)
*angulata* Loew
*angustipennis* Loew
*bella* Loew
*bicornis* Forbes
*caloptera* Loew
*cincticornis* Doane
*collaris* Say
*dejecta* Walk.
*eluta* Loew
*grata* Loew
*hebes* Loew
*hermannia* Alex.
*iroquois* Alex.
*latipennis* Loew
*macrolabis* Loew
*megaura* Doane
*retorta* v. d. W.

*Tipula sayi* Alex.
*senega* Alex.
*serta* Loew
*sulphurea* Doane
*tephrocephala* Loew
*Tipula trivittata* Say
*ultima* Alex.
*umbrosa* Loew
*valida* Loew
*vitrea* v. d. W.

**Newfoundland**

(The Owen Bryant collections in the cabinet of C. W. Johnson)

*Bittacomorpha clavipes* (Fabr.)
*Erioptera chlorophylla* O. S.
*Limnophila rufibasis* O. S.
*terrae-novae* Alex.
*Tricyphona inconstans* (O. S.)
*Nephrotoma vittula* (Loew)
*Tipula abdominalis* (Say)
*hermannia* Alex.
*mainensis* Alex.
*trivittata* Say
*umbrosa* Loew
*valida* Loew

**Labrador**

(Many of the types of Loew and Alexander, collected by Packard, Schneider, and Bryant)

*Dicranomyia halterata* O. S.
*Tricyphona hyperborea* (O. S.)
*Dolichopeza americana* Needm.
*Tipula angustipennis* Loew
*imperfecta* Alex.
*labradorica* Alex.
*septentrionalis* Loew

**Washington, D. C., and vicinity**

This remarkable local list is added here to indicate the southern species that may range into our limits. The pioneer collecting of Osten Sacken has been thoroly supplemented by that of W. L. McAtee, R. C. Shannon, Frederick Knab, and some others.

*Ptychoptera rufocincta* O. S.
*Bittacomorpha clavipes* (Fabr.)
*Bittacomorphella jonesi* (Johns.)
*Trichocera* sp.
*Discobola argus* (Say)
*Dicranomyia badia* (Walk.)
*brevivena* O. S.
*distans* O. S.
*diversa* O. S.
*floridana* O. S.
*gladiator* O. S.
*globithorax* O. S.
*haeretica* O. S.
*immodesta* O. S.
*liberta* O. S.
*Dicranomyia macateei* Alex.
*morioides* O. S.
*pubipennis* O. S.
*rara* O. S.
*simulans* (Walk.)
*Geranomyia canadensis* (Westw.)
*rostrata* (Say)
*Limnobia cinctipes* Say
*immatura* O. S.
*indigena* O. S.
*triocellata* O. S.
*tristigma* O. S.
*Rhipidia bryanti* Johns.
*domestica* O. S.
*fidelis* O. S.
*maculata* Meig.
*shannoni* Alex.

*Antocha saxicola* O. S.

*Atarba picticornis* O. S.

*Elephantomyia westwoodi* O. S.

*Dicranoptycha sobrina* O. S.
*winnemana* Alex.

*Rhamphidia flavipes* Macq.
*mainensis* Alex.

*Teucholabis complexa* O. S.
*lucida* Alex.

*Toxorhina muliebris* (O. S.)

*Cladura flavoferruginea* O. S.

*Erioptera armata* O. S.
*armillaris* O. S.
*caloptera* Say
*chlorophylla* O. S.
*chrysocoma* O. S.
*graphica* O. S.
*needhami* Alex.
*noctivagans* Alex.
*parva* O. S.
*septemtrionis* O. S.
*venusta* O. S.
*vespertina* O. S.

*Gnophomyia luctuosa* O. S.
*tristissima* O. S.

*Gonomyia blanda* O. S.
*cognatella* O. S.
*manca* (O. S.)
*subcinerea* O. S.
*sulphurella* O. S.

*Helobia hybrida* (Meig.)

*Molophilus hirtipennis* (O. S.)
*nova-caesariensis* Alex.
*pubipennis* (O. S.)
*ursinus* (O. S.)

*Ormosia holotricha* (O. S.)
*innocens* (O. S.)
*nigripila* (O. S.)
*nubila* (O. S.)

*Trimicra anomala* O. S.

*Adelphomyia americana* Alex.

*Epiphragma fascipennis* (Say)
*solatrix* (O. S.)

*Limnophila adusta* O. S.
*aprilina* O. S.
*areolata* O. S.
*brevifurca* O. S.
*contempta* O. S.
*emmelina* Alex.
*fuscovaria* O. S.
*lenta* O. S.
*luteipennis* O. S.
*macrocera* (Say)
*montana* O. S.
*mundoides* Alex.
*nigripleura* A. & L.
*quadrata* O. S.
*recondita* O. S.
*rufibasis* O. S.
*tenuipes* (Say)
*terebrans* Alex.
*toxoneura* O. S.
*ultima* O. S.

*Ula paupera* O. S.

*Eriocera cinerea* Alex.
*fuliginosa* O. S.
*longicornis* (Walk.)
*tristis* Alex.
*wilsonii* O. S.

*Hexatoma megacera* (O. S.)

*Penthoptera albitarsis* O. S.

*Dicranota eucera* O. S.
*noveboracensis* Alex.
*rivularis* O. S.

*Pedicia albivitta* Walk.

*Rhaphidolabis tenuipes* O. S.

*Tricyphona inconstans* (O. S.)
*vernalis* (O. S.)

*Liogma nodicornis* (O. S.)

*Brachypremna dispellens* (Walk.)

*Oropeza albipes* Johns.
*dorsalis* Johns.
*obscura* Johns.
*sayi* Johns.
*subalbipes* Johns.

*Tanyptera frontalis* (O. S.)

*Longurio testaceus* Loew

*Nephrotoma eucera* (Loew)
*ferruginea* (Fabr.)
*incurva* (Loew)
*macrocera* (Say)
*occipitalis* (Loew)
*polymera* (Loew)
*tenuis* (Loew)

*Nephrotoma virescens* (Loew)
*xanthostigma* (Loew)

*Tipula abdominalis* (Say)
*annulicornis* Say
*australis* Doane
*bella* Loew
*bicornis* Forbes
*caloptera* Loew
*collaris* Say
*cunctans* Say
*dejecta* Walk.
*dietziana* Alex.
*eluta* Loew
*fragilis* Loew
*fraterna* Loew
*fuliginosa* (Say)
*hebes* Loew
*hermannia* Alex.
*ignobilis* Loew
*iroquois* Alex.
*johnsoniana* Alex.
*longiventris* Loew
*mingwe* Alex.
*morrisoni* Alex.
*perlongipes* Johns.
*sayi* Alex.
*submaculata* Loew
*tricolor* Fabr.
*triton* Alex.
*trivittata* Say
*tuscarora* Alex.
*ultima* Alex.
*umbrosa* Loew

## *The crane-flies of New York*

The fact that New York has a known crane-fly fauna which is larger and better-developed than that of any other State in the Union, is due, in large part, to the diversity of natural conditions, which range from high mountains to sea level and include lakes, rivers, swamps, bogs, woodlands, gorges, ravines, and most other haunts that attract these insects. Another reason for this exceptional list is the fact that the State has long been a favorite collecting ground for many students of crane-flies, and a large number of species were first characterized from material taken in New York. These include species described by Osten Sacken, Loew, Doane, Johnson, Needham, Dietz, and Alexander. The pioneer collector, Baron Osten Sacken, did much of his collecting in this State, especially in the Adirondacks at Trenton Falls, in the Schoharie Valley at Sharon Springs, in the vicinity of New York City, and later in the Catskills. His work furnished the basis for Needham's preliminary list (Needham, 1908:203–211), which includes one hundred and four species known from New York at that time. Subsequent collecting in various parts of the State has considerably increased the number of species, so that comparatively few additions may be expected. The more probable of these have been indicated in the following list under the heading *Regional species.*

In this list the type localities are designated by the initials *T. L.* The published records of Needham (1908:203–211) and of Alexander (1910 and 1912) have been largely included, altho some of the records for

common and widely distributed species have been omitted. Similarly, many records for Erie, Fulton, and Tompkins Counties have been abbreviated or omitted, since their inclusion would but lengthen the paper and add little to the data; such records are indicated by "etc."

Fulton County, with a known crane-fly fauna of more than two hundred species, probably has the largest local list as known for any region of similar size in the world. The other counties that are well known are Tompkins, Cortland, Herkimer (Osten Sacken, Needham, and Alexander), Albany (Young), and Erie (Van Duzee). Considerable data from Hamilton County (Young), Genesee County (Knight), and Chenango County, are likewise available. The region around New York City is not completely known, the most valuable collections from that section being those made by Frost in Westchester County and by Banks in Nassau County.

The following abbreviations to express collectors are used in this list:

| | |
|---|---|
| A. C. C. | A. C. Coutant |
| A. D. M. | A. D. MacGillivray |
| A. H. M. | Miss A. H. Morgan |
| A. L. M. | Axel L. Melander |
| A. M. | A. MacDonald |
| A. M. N. | A. M. Nadler |
| A. O. | Axel Olsson |
| A. P. M. | A. P. Morse |
| C. H. K. | C. H. Kennedy |
| C. I. | Carl Ilg |
| C. O. H. | C. O. Houghton |
| C. P. A. | C. P. Alexander |
| C. R. C. | C. R. Crosby |
| C. R. P. | C. R. Plunkett |
| D. B. Y. | D. B. Young |
| E. M. | Miss E. Moore |
| E. T. W. | Mrs. W. C. Woods |
| F. K. | Fritz Kahn |
| F. N. H. | F. N. Harvey |
| H. E. S. | H. E. Schradieck |
| H. H. K. | H. H. Knight |
| H. H. S. | H. H. Smith |
| H. Y. | Hachiro Yuasa |
| J. A. L. | J. A. Lintner |
| J. C. B. | J. Chester Bradley |
| J. C. F. | J. C. Faure |
| J. G. N. | J. G. Needham |
| J. L. Z. | J. L. Zabriskie |
| J. S. | J. Silver |
| J. T. L. | J. T. Lloyd |
| L. W. C. | Mrs. W. A. Clemens |
| M. C. VD. | M. C. Van Duzee |
| M. D. L. | M. D. Leonard |
| M. M. A. | Mrs. C. P. Alexander |
| N. B. | Nathan Banks |
| O. A. J. | O. A. Johannsen |
| O. S. | Osten Sacken |
| P. W. C. | P. W. Claassen |
| R. C. S. | R. C. Shannon |
| R. F. P. | R. F. Pearsall |
| R. H. P. | R. H. Pettit |
| R. H. T. | Mrs. J. D. Tothill |
| S. A. G. | S. A. Graham |
| S. C. B. | S. C. Bishop |
| S. W. F. | S. W. Frost |
| W. A. C. | W. A. Clemens |
| W. A. H. | W. A. Hoffman |
| W. A. R. | W. A. Riley |
| W. D. F. | W. D. Funkhouser |
| W. P. A. | W. P. Alexander |
| W. S. | W. Sheffield |
| W. T. M. F. | W. T. M. Forbes |

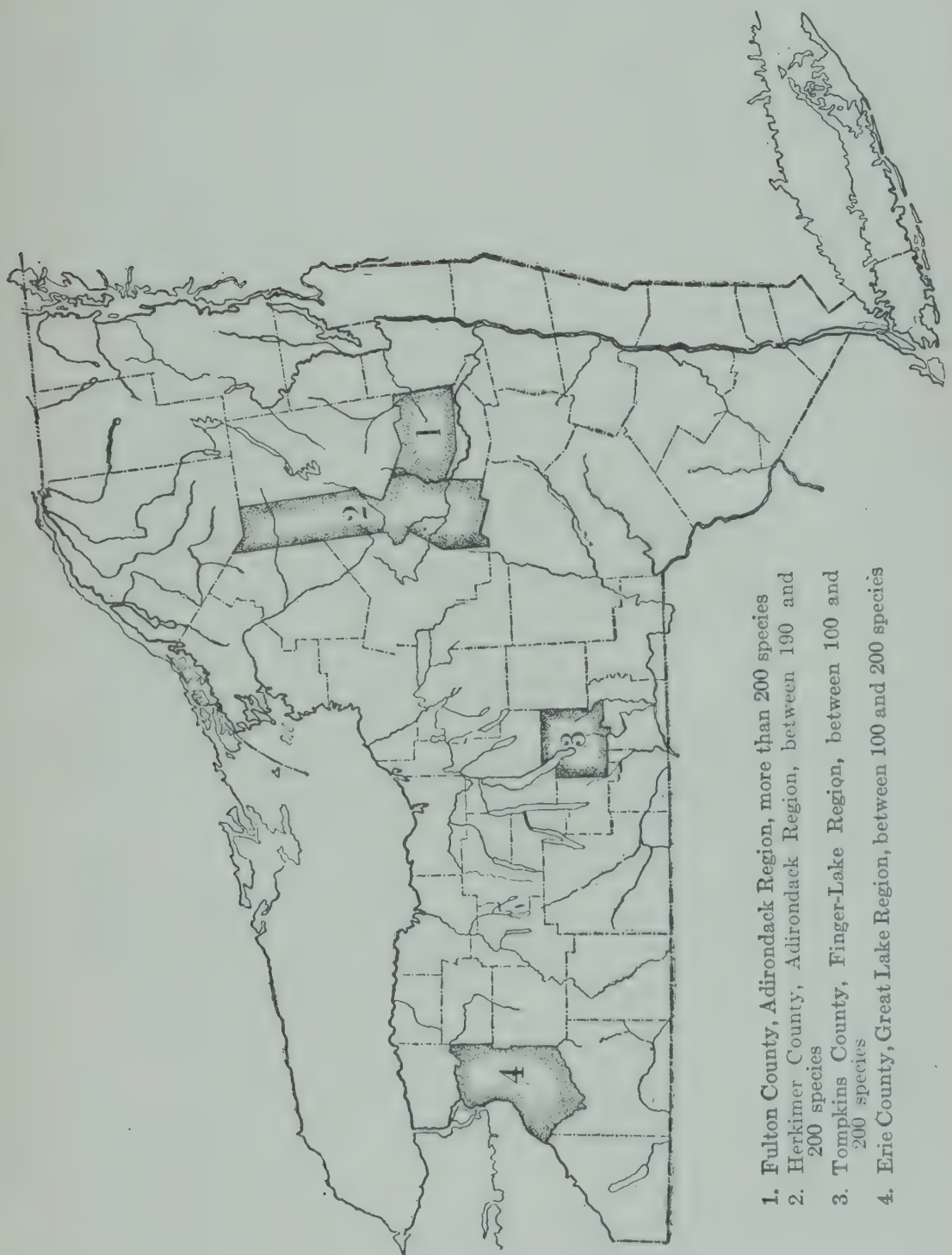
1
2
3
4
1. Fulton County, Adirondack Region, more than 200 species
2. Herkimer County, Adirondack Region, between 190 and 200 species
3. Tompkins County, Finger-Lake Region, between 100 and 200 species
4. Erie County, Great Lake Region, between 100 and 200 species

FIG. 121. COUNTIES IN NEW YORK STATE IN WHICH CONSIDERABLE COLLECTIONS OF CRANE-FLIES HAVE BEEN MADE

## Family Tanyderidae

Genus *Protoplasa* Osten Sacken

*Protoplasa fitchii* O. S.

Fulton County: Sport Island, Sacandaga River, altitude 750 feet, June 6–19 (C. P. A.).

(Fitch's type locality is New York State.)

## Family Ptychopteridae

### Subfamily Ptychopterinae

Genus *Ptychoptera* Meigen

*Ptychoptera rufocincta* O. S.

Chautauqua County: Dunkirk, July 5.
Dutchess County: Poughkeepsie, May 24 (D. B. Y.).
Erie County: Hamburg, June 6 to July 10 (M. C. VD.); Colden, June 7 (M. C. VD.); East Aurora, June 11 to August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.).
Genesee County: Batavia, June 19 (H. H. K.).
Nassau County: Sea Cliff (N. B.).
Onondaga County: Manlius, August 29 (H. H. S.).
Suffolk County: Yaphank, May 20.
Tompkins County: Ithaca, May 31 to July 5 (C. P. A.).
Westchester County: Dobbs Ferry (O. S.), T. L.
Wyoming County: Portage Falls, July 27 (H. H. K.).

### Subfamily Bittacomorphinae

Genus *Bittacomorpha* Westwood

*Bittacomorpha clavipes* (Fabr.)

Cattaraugus County: Little Valley, August 7 (M. C. VD.).
Cayuga County: North Fair Haven, May 17 (E. M. and J. G. N.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Dutchess County: Poughkeepsie, July 18 (S. W. F.).
Erie County: Colden, May 23-30 (M. C. VD.); Hamburg, June 6 (M. C. VD.); etc.
Fulton County: Sacandaga Park, etc., June 13 to September 13 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August 21 (J. G. N.).
Nassau County: Sea Cliff (N. B.).
Oneida County: McMullen's Brook, May 20 (W. A. C.).
Onondaga County: Manlius, September 23 (H. H. S.).
Suffolk County: Yaphank, May 29–30; Bellport, August 9.
Tompkins County: Ithaca, May 20 to September 28 (C. P. A.); etc.
Warren County: Paradise Bay, Lake George, August 24.

Genus *Bittacomorphella* Alexander

*Bittacomorphella jonesi* (Johns.)

Albany County: Karner, June 19 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 11–28 (C. P. A.); Mountain Lake, June 13–24 (C. P. A.); etc.
Tompkins County: Ithaca, Bool's, July 13–19 (C. P. A.).

## Family Rhyphidae

### Subfamily Trichocerinae

Genus *Trichocera* Meigen
Subgenus *Trichocera* Meigen
*Trichocera bimacula* Walk.
Erie County: Gowanda, October 4 (M. C. VD.); East Aurora, October 20 (M. C. VD.).
Fulton County: Gloversville, September 15 (C. P. A.); etc.
Tompkins County: Ithaca, May 20, October 15 (C. P. A.); etc.
*T. brumalis* Fitch
Fulton County: Gloversville, September 25 to October 15 (C. P. A.); etc.
Tompkins County: Ithaca, September 30 to October 30 (C. P. A.); etc.
Subgenus *Diazosma* Bergroth
*Trichocera subsinuata* Alex.
Fulton County: Woodworth's Lake, altitude 1650 feet, June 15 (C. P. A.), T. L.

### Subfamily Rhyphinae

Genus *Rhyphus* Latreille
*Rhyphus alternatus* Say
Albany County: Albany.
Erie County: East Aurora, May.
Franklin County: Axton, June.
Tompkins County: Ithaca, May to June (O. A. J.).
*R. fenestralis* (Scop.)
Erie County: Hamburg, April.
Oneida County: New Hartford, April.
Tompkins County: Ithaca, April to May (O. A. J.).
*R. punctatus* (Fabr.)
Erie County.
Fulton County: Johnstown.
Tompkins County: Ithaca, May to October (O. A. J.).

### Subfamily Mycetobiinae

Genus *Mycetobia* Meigen
*Mycetobia divergens* Walk.
Albany County: Albany.
Tompkins County: Ithaca, May (O. A. J.).

## Family Tipulidae

### Subfamily Limnobiinae

Tribe Limnobiini

Genus *Dicranomyia* Stephens
*Dicranomyia badia* (Walk.)
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Boston, July 10 (M. C. VD.); East Aurora, September 20 (M. C. VD.); etc.
Fulton County: Gloversville, June 3 (C. P. A.); Sacandaga Park, June 5 (C. P. A.); etc.

Genus *Dicranomyia* Stephens (*continued*)

*Dicranomyia badia* (Walk) (*continued*)

Hamilton County: Augur Flats, July 17 (D. B. Y.); Wells, July 29 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.).
Nassau County: Sea Cliff, April (N. B.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).
Schoharie County: Sharon Springs (O. S.).
Tompkins County: Ithaca, May 4 to November 10 (C. P. A.); etc.

*D. brevivena* O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Lancaster, June 22 (M. C. VD.); Buffalo, September 30 (M. C. VD.).
Fulton County: Sulphur Spring Junction, September (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, October 9 (M. C. VD.).

*D. gladiator* O. S.

Fulton County: Woodworth's Lake, August 22 (C. P. A.).

*D. globithorax* O. S.

Erie County: Boston, September 3 (M. C. VD.).
Fulton County: Woodworth's Lake, August 4–22 (C. P. A.); etc.
Tompkins County: Ellis Hollow, May 14 (C. P. A.); Ithaca, September 28 (J. G. N.).

*D. haeretica* O. S.

Erie County: Buffalo, October 14 (M. C. VD.).
New York: On salt marshes near New York (O. S.), T. L.
Suffolk County: Cold Spring Harbor, July 15 (A. L. M.); Bellport, August 19 (C. P. A.).

*D. halterata* O. S.

Fulton County: Johnstown, September 15 (C. P. A.); Mud Lake, September 18 (C. P. A.).

*D. immodesta* O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.)
Erie County: Buffalo, October 3–15 (M. C. VD.).
Fulton County: Gloversville, June 9 (C. P. A.); Johnstown, September 15 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9–13 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: Ithaca, June 20 (C. P. A.); McLean, September 28 (C. P. A.); etc.

*D. liberta* O. S.

Albany County: Karner, May 22 (D. B. Y.); Albany, June 2–19 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Hamburg, May 28 to September 11 (M. C. VD.); Lancaster, June 4 to August 14 (M. C. VD.); Buffalo, June 12 to August 25 (M. C. VD.); etc.
Fulton County: Gloversville, June 10 to September 20 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
New York: (O. S.), T. L.
Onondaga County: Green Lake, June 8 (C. P. A.).
Suffolk County: Bellport, July 1.
Tompkins County: Ithaca, May 22 to June 20 (C. P. A.); etc.
Westchester County: Tarrytown, June 25 (S. W. F.).

Genus *Dicranomyia* Stephens (*continued*)

*D. longipennis* (Schum.)
Erie County: Hamburg, September 11 (M. C. VD.).
Fulton County: Hillside Park, August 4 (C. P. A.); Sacandaga Park, August 24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.).
Nassau County: Sea Cliff (N. B.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, June 20 to August 1 (C. P. A.); McLean, September 28 (C. R. C.).

*D. macateei* Alex.
Fulton County: Sylvan Lake, June 15 (C. P. A.); Mountain Lake, July 7 (C. P. A.).

*D. moniliformis* Doane
Suffolk County: Long Island, T. L.

*D. monticola* (Alex.)
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Gloversville, June 24 (C. P. A.).
Hamilton County: Wells, July 23–30 (D. B. Y.).
Tompkins County: Ithaca, reared June 3 (C. P. A.).

*D. morioides* O. S.
Erie County: Hamburg, May 3 (M. C. VD.).
Fulton County: Mayfield Mountain, June 21 (C. P. A.); Northampton, June 25 (D. B. Y.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Trenton Falls, July (O. S.), T. L.
Tompkins County: McLean, May 13 (C. P. A.); Ithaca, May 18 to August 26 (C. P. A.).

*D. pubipennis* O. S.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Buffalo, June 9 (M. C. VD.); Boston, September 3 (M. C. VD.); etc.
Fulton County: Mountain Lake, June 17 to July 7 (C. P. A.); Gloversville, September 16 (C. P. A.); etc.
Hamilton County: Wells, July 7–25 (D. B. Y.).
Nassau County: Sea Cliff, June (N. B.).
Tompkins County: Ithaca, August 1 (C. P. A.); etc.
Westchester County: Tarrytown, June 9–16 (S. W. F.).

*D. pudica* O. S.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: North Evans, May 14 (M. C. VD.); East Aurora, May 18 (M. C VD.); Lancaster, May 31 (M. C. VD.); Boston, July 10 (M C. VD.); etc.
Fulton County: Sylvan Lake, June 15 (C. P. A.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, June.

*D. rara* O. S.
Genesee County: Batavia, September 28 (H. H. K.).
New York: (O. S.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).

*D. rostrifera* O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).

Genus *Dicranomyia* Stephens (*continued*)
*D. rostrifera* O. S. (*continued*)
Fulton County: Sacandaga Park, June 27 to August 28 (C. P. A.); Sammonsville, September 22 (C. P. A.); etc.
New York: (O. S.), T. L.
*D. simulans* (Walk.)
Albany County: Helderbergs, July 3 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, June 23 (M. C. VD.); South Wales, June 23 to July 9 (M. C. VD.); etc.
Fulton County: Dolgeville, May 16 (C. P. A.).
Herkimer County: Trenton Falls (O. S.); Old Forge, July 16 (J. G. N.).
Nassau County: Sea Cliff, July (N. B.).
Oneida County: Tannery Brook, July 12 (W. A. C.).
Tompkins County: Ithaca, May 30 to November 14 (C. P. A.); etc.
Westchester County: Tarrytown, August 1 (S. W. F.).
*D. stulta* O. S.
Fulton County: Mountain Lake, June 14 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, reared from larvae, June 1 (C. P. A.); abundant along Cascadilla Creek, June 13–18 (C. P. A.).

Genus *Geranomyia* Haliday
*Geranomyia canadensis* (Westw.)
Erie County: Lancaster, June 8 to August 15 (M. C. VD.); East Aurora, August 24 (M. C. VD.); Hamburg, September 11 (M. C. VD.); etc.
Fulton County: Canada Lake, June 23 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).
Onondaga County: Manlius, August 20 (H. H. S.).
Tompkins County: Ithaca, May 7 to October 13 (C. P. A.).
*G. diversa* O. S.
Erie County: Springville, August 12 (M. C. VD.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, May 12 to August 26 (C. P. A.).
*G. rostrata* (Say)
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Colden, May 30 to August 9 (M. C. VD.); Gowanda, August 22 (M. C. VD.); etc.
Fulton County: Mount Buell, June 15 (C. P. A.); Sacandaga Park, August 24 (C. P. A.).
New York: (O. S.).
Tompkins County: Ithaca, August 27 (A. C. C.).

Genus *Rhipidia* Meigen
Subgenus *Rhipidia* Meigen
*Rhipidia bryanti* Johns.
Erie County: East Aurora, June 15 (M. C. VD.).
*R. maculata* Meig.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Essex County: Wilmington, August 24 (J. C. B.).
Fulton County: Woodworth's Lake, September 2 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.); Old Forge, July 6–20 (J. G. N.).
Tompkins County: McLean, June 5 (C. P. A.).

Genus *Rhipidia* Meigen (*continued*)
Subgenus *Monorhipidia* Alexander
*Rhipidia fidelis* O. S.
Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: Gowanda, June 15 (M. C. VD.).
Fulton County: Sacandaga Park, June 15–27 (C. P. A.); etc.
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, May 15 (C. I.); McLean, June 5 (C. P. A.).

Genus *Limnobia* Meigen
*Limnobia cinctipes* Say
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: East Aurora, May 7 (M. C. VD.).
Essex County: New Russia, August (J. C. B.); Keene Valley, August 14 (J. A. L.).
Fulton County: Dolgeville, May 16 (A. O.); Mount Buell, June 13 (C. P. A.); etc.
Hamilton County: Saranac Inn, June 17 (J. G. N.); Augur Flats, July 17 (D. B. Y.).
Herkimer County: Old Forge, July 29 (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 4 (C. P. A.).
Warren County: Lake George, August 29 (J. L. Z.).
*L. fallax* Johns.
Genesee County: Batavia, May 22 (H. H. K.).
Tompkins County: Ithaca, reared July 21 (O. A. J.).
*L. immatura* O. S.
Albany County: Albany, June 4 (D. B. Y.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 18 (C. P. A.).
Herkimer County: Old Forge, June 17 (J. G. N.).
Tompkins County: McLean, July 27 (H. H. K.).
*L. indigena* O. S.
Cattaraugus County: Rock City, June 6 (J. C. B.); Little Valley, June 30 (M. C. VD.).
Erie County: Gowanda, June 27 (M. C. VD.); North Evans, July 4 to October 22 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 13 (C. P. A.); Mayfield Mountain, September 20 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Old Forge, June 17 to August (J. G. N.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Onondaga County: Manlius, September 1 (H. H. S.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tompkins County: Ithaca, May 24–29 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
*L. parietina* O. S.
Erie County: Boston, September 3 (M. C. VD.).
Fulton County: Woodworth's Lake, August 20 (C. P. A.).
Hamilton County: Silver Lake, September 2 (C. P. A.); Big Notch Mountain, Hope Township, September 12 (C. P. A.).
Herkimer County: Old Forge, August 15 (J. G. N.); Trenton Falls, September (O. S.), T. L.
Tompkins County: Needham's Glen, Ithaca, September 17 (J. G. N.).

Genus *Limnobia* Meigen (*continued*)

*L. solitaria* O. S.

Erie County: (M. C. Van Duzee records *L. hudsonica* from Spring Brook, June 26, 1911. In the absence of specimens this record should be questioned, inasmuch as this is a variable species and close to *solitaria*.)
Essex County: Keene Valley, July 17 (J. A. L.).
Fulton County: Gloversville, June 9 (C. P. A.); Pinnacle Mountain, August 5 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 6 to June 20 (C. P. A.).
Ulster County: Catskills, July (O. S.).

*L. triocellata* O. S.

Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Gowanda, June 13–14 (M. C. VD.); Hamburg, August 10 (M. C. VD.); etc.
Fulton County: Woodworth's Lake, August 22 (C. P. A.); etc.
Hamilton County: Elm Lake, August 7 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.), T. L.
Onondaga County: Manlius, September 1 (H. H. S.).
Putnam County: Highlands, October 3 (J. S.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, August 25 (W. D. F.).

*L. tristigma* O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Essex County: Elizabethtown, August 12 (D. B. Y.).
Fulton County: Gloversville, July 3 (C. P. A.); Woodworth's Lake, August 24 (C. P. A.); etc.
Hamilton County: Dug Mountain, August 8 (D. B. Y.).
Herkimer County: Old Forge, August 15 (J. G. N.).
Niagara County: Niagara Falls, July 20 (M. C. VD.).
Rensselaer County: Brookview, July 13 (M. M. A.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).

Genus *Discobola* Osten Sacken

*Discobola argus* (Say)

Albany County: Karner, October 17 (D. B. Y.).
Cattaraugus County: Little Valley, July 31 (M. C. VD.).
Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).
Erie County: East Aurora, June 11–22 (M. C. VD.); Gowanda, October 4 (M. C. VD.); Hamburg, October 16 (M. C. VD.); etc.
Essex County: New Russia, August (J. C. B.); Mount Whiteface, altitude 4800 feet, August 24 (C. R. C. and W. T. M. F.).
Fulton County: Green Lake, June 25 (C. P. A.); Gloversville, September 20 (C. P. A.); etc.
Genesee County: Batavia, June 18 (H. H. K.).
Hamilton County: Saranac Inn, July 30 (J. G. N.); Wells, August 3 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.); Old Forge, August 23 (J. G. N.).
Monroe County: Rochester, October 10 (M. C. VD.).
Nassau County: Sea Cliff, May (N. B.).
Tompkins County: Ithaca, August 7 to October 3 (C. I.); etc.
Yates County: Keuka Park, October 29 (C. R. C.).

Regional species: *Dicranomyia brunnea* Doane, *D. diversa* O. S., *D. isabellina* Doane, *Geranomyia distincta* Doane, *Limnobia sociabilis* O. S., *Rhipidia domestica* O. S., *R. shannoni* Alex.

Tribe **Antochini**

Genus *Rhamphidia* Meigen

*Rhamphidia flavipes* Macq.

Albany County: Albany, July 19 (D. B. Y.).
Erie County: Buffalo, May 28 (M. C. VD.).
Fulton County: Sacandaga Park, June 2 to August 24 (C. P. A.); etc.
New York: (O. S.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 29 to August 7 (C. P. A.); etc.

*R. mainensis* Alex.

Tompkins County: Larch Meadows, Ithaca, reared May 14 (C. P. A.).

Genus *Elephantomyia* Osten Sacken

*Elephantomyia westwoodi* O. S.

Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Hamburg, July 10 (M. C. VD.); Springville, July 12 (M. C. VD.).
Fulton County: Mountain Lake, June 24 to August 13 (C. P. A.); etc.
Hamilton County: Wells, July 30 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.), T. L.; Old Forge, August 3 (J. G. N.).
Ulster County: Catskills, July, 1874 (O. S.).

Genus *Toxorhina* Loew

*Toxorhina muliebris* (O. S.)

Erie County: Hamburg, July 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.).
Suffolk County: Yaphank, June 28 (A. M. N.).
Tompkins County: Ithaca (R. H. T.); McLean, July 3 (A. D. M.).

Genus *Dicranoptycha* Osten Sacken

*Dicranoptycha germana* O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.).
Hamilton County: Augur Flats, July 17 (D. B. Y.); Wells, July 30 (D. B. Y.).
Herkimer County: Trenton Falls, July (O. S.), T. L.; Old Forge, July 6–24 (J. G. N.).
Onondaga County: Manlius, July 25 (H. H. S.).
Tompkins County: Ithaca, July 13 (C. P. A.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).

*D. sobrina* O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Fulton County: Mayfield Mountain, September 20 (C. P. A.).
Tompkins County: Ithaca, August 30 (J. G. N.).

Genus *Antocha* Osten Sacken

*Antocha saxicola* O. S.

Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, June 2 (M. C. VD.); Buffalo, June 15 (M. C. VD.).
Fulton County: Sacandaga Park, June 11 to July 3 (C. P. A.); etc.

Genus *Antocha* Osten Sacken (*continued*)
*Antocha saxicola* O. S. (*continued*)
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.); Newport, June 9 to July 27 (D. B. Y.); Old Forge, July 16 (J. G. N.).
Monroe County: Honeoye Falls, May 15 (M. D. L.); September 1 (C. R. C.).
Oneida County: Tannery Brook, July 12 (W. A. C.).
Onondaga County: Manlius, August 20 (H. H. S.).
Rensselaer County: Brookview, July 16 (M. M. A.).
Tioga County: Willseyville, May 25 (W. A. H.).
Tompkins County: Ithaca, May 13 to September 25 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
Wyoming County: Portage, May 24 (H. H. K.).

Genus *Atarba* Osten Sacken
*Atarba picticornis* O. S.
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9–13 (M. C. VD.).
Fulton County: Sacandaga Park, June 28 (C. P. A.).
Herkimer County: Trenton Falls, July (O. S.).
Suffolk County: Bellport, July 5.

Genus *Teucholabis* Osten Sacken
*Teucholabis complexa* O. S.
Herkimer County: Trenton Falls, June (O. S.), T. L.

Regional species: *Dicranoptycha nigripes* O. S., *D. winnemana* Alex., *Teucholabis lucida* Alex., *Toxorhina magna* (O. S.).

Tribe Eriopterini

Genus *Ormosia* Rondani
*Ormosia apicalis* Alex.
Fulton County: Mountain Lake, June 17 (C. P. A.).
Tompkins County: Ithaca, August 8 (J. G. N.).
*O. arcuata* (Doane)
Erie County: Hamburg, May 7 (M. C. VD.).
Tompkins County: Ithaca, T. L.
*O. bilineata* Dietz
Erie County: Holland, May 21–25 (M. C. VD.), T. L.
*O. deviata* Dietz
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Hamburg, May 26 (M. C. VD.), T. L.
Fulton County: Mountain Lake, June 1–18 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*O. holotricha* (O. S.).
Fulton County: Johnstown, May 14 (C. P. A.).
Tompkins County: Ithaca, April 27 to May 22 (C. P. A.); Taughannock, May 4 (C. P. A.).
*O. innocens* (O. S.).
Albany County: Albany, May 8 (D. B. Y.).
Erie County: Hamburg, May 28 (M. C. VD.).

Genus *Ormosia* Rondani (*continued*)

*O. innocens* (O. S.) (*continued*)
Nassau County: Sea Cliff (N. B.).
Tompkins County: Ithaca, April 24 to May 25 (C. P. A.); McLean, May 13 (C. P. A.).

*O. megacera* Alex.
Fulton County: Gloversville, June 22 (C. P. A.), T. L.

*O. meigenii* (O. S.)
Erie County: Colden, May 29 (M. C. VD.).
Fulton County: Johnstown, May 14 (C. P. A.); Gloversville, June 3 (C. P. A.); etc.
Tompkins County: Ithaca, April 26 to May 12 (C. P. A.); McLean, May 13 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

*O. mesocera* Alex.
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Gloversville, June 22 (C. P. A.), T. L.

*O. monticola* (O. S.)
Erie County: Colden, August 7 (M. C. VD.).
Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Sacandaga Park, August 24 (C. P. A.).
Hamilton County: Speculator, August 5 (D. B. Y.).
Herkimer County: Old Forge, August (J. G. N.).
Tompkins County: Ithaca, August 26 (C. P. A.).

*O. nigripila* (O. S.)
Fulton County: Mountain Lake, June 13 (C. P. A.); Pinnacle, August 5 (C. P. A.).
Nassau County: Sea Cliff, May (N. B.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: McLean, May 22 (H. E. S.); Ithaca, May 31 (R. H. T.).
Westchester County: Tarrytown, June 9 (S. W. F.).

*O. nimbipennis* Alex.
Fulton County: Woodworth's Lake, August 13 (C. P. A.), T. L.
Hamilton County: Wells, July 29 (D. B. Y.).

*O. nubila* (O. S.)
Albany County: Albany, May 8 (D. B. Y.).
Erie County: Colden, August 7 (M. C. VD.); Boston, September 3 (M. C. VD.); Lancaster, September 24 to October 18 (M. C. VD.); etc.
Fulton County: Johnstown, May 14 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.
Nassau County: Sea Cliff, May (N. B.).
Tompkins County: Ithaca, April 24 to May 16 (C. P. A.); McLean, May 13 (C. P. A.).

*O. parallela* (Doane)
Tompkins County: Ithaca, T. L.

*O. perplexa* Dietz
Erie County: Waverly, May (M. C. VD.), T. L.

*O. pygmaea* (Alex.)
Erie County: Hamburg, May 28 (M. C. VD.).
Fulton County: Woodworth's Lake, August 22 (C. P. A.), T. L.
Tompkins County: Ithaca, May 28 (W. S.).

*O. rubella* (O. S.)
Erie County: Colden, August 7 (M. C. VD.); Lancaster, September 24 to October 18 (M. C. VD.); etc.

Genus *Ormosia* Rondani (*continued*)
*O. rubella* (O. S.) (*continued*)
Fulton County: Mayfield Mountain, September 20 (C. P. A.); etc.
Niagara County: Niagara Falls, September 8 to October 17 (M. C. VD.).
Orange County: West Point (O. S.), T. L.

Genus *Erioptera* Meigen
Subgenus *Erioptera* Meigen
*Erioptera chlorophylla* O. S.
Albany County: Albany, June 28 (D. B. Y.).
Erie County: Gowanda, June 15 (M. C. VD.); South Wales, July 13 (M. C. VD.); Hamburg, July 27 (M. C. VD.); etc.
Franklin County: Saranac Inn, July 4 (J. G. N.).
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Herkimer County: Old Forge, July 29 (J. G. N.).
Queens County: Flushing, June 22 (C. R. P.); Little Ferry, August 15 (C. R. P.).
Tompkins County: Ithaca, July 10–13 (C. P. A.).
*E. chrysocoma* O. S.
Fulton County: Mountain Lake, June 15 to July 7 (C. P. A.); Sacandaga Park, June 18 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*E. megophthalma* Alex.
Fulton County: Sacandaga Park, June 18 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9–13 (C. P. A.).
Tompkins County: Ithaca, May 28 to June 13 (C. P. A.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).
*E. septemtrionis* O. S.
Erie County: Gowanda, June 7 (M. C. VD.); East Aurora, June 11 (M. C. VD.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Mount Buell, June 5–18 (C. P. A.); Mountain Lake, August 13 (C. P. A.); etc.
Herkimer County: Old Forge, July 17–21 and in August (J. G. N.).
Madison County: Canastota (J. C. F.).
Oneida County: Lee Center, July 24 (W. A. C.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, April 26 to July 13 (C. P. A.); McLean, May 13 to June 5 (C. P. A.).
*E. straminea* O. S.
Erie County: Gowanda, June 14–27 (M. C. VD.); Grand Island, June 26 (M. C. VD.).
Fulton County: Sacandaga Park, June 18 (C. P. A.).
*E. vespertina* O. S.
Cattaraugus County: Chipmunk Swamp, Vandalia, June 9 (C. R. C.).
Erie County: Hamburg, June 20 (M. C. VD.).
Fulton County: Sacandaga Park, June 5–28 (C. P. A.); etc.
Tompkins County: Ithaca, May 15 to July 13 (C. P. A.); etc.
*E. villosa* O. S.
Erie County: Holland, May 21 (M. C. VD.); North Evans, May 29 (M. C. VD.); Buffalo, June 23 to July 9 (M. C. VD.); Spring Brook, June 25 (M. C. VD.); Gowanda, June 27 (M. C. VD.).

Genus *Erioptera* Meigen (*continued*)

Subgenus *Acyphona* Osten Sacken

*Erioptera armillaris* O. S.

Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Elma, August 24 (M. C. VD.).
Fulton County: Sacandaga Park, June 11–18 (C. P. A.); Mountain Lake, June 17 to July 7 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, August 30 (C. P. A.).

*E. graphica* O. S.

Tompkins County: Ithaca, July 13 (H. Y.), August 2–7 (C. P. A.).

*E. venusta* O. S.

Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 to September 20 (D. B. Y.).
Erie County: Gowanda, June 7–27 (M. C. VD.); Hamburg, June 18–20 (M. C. VD.); Colden, August 16 (M. C. VD.); etc.
Fulton County: Gloversville, June 3 to September 20 (C. P. A.); etc.
Genesee County: Batavia, July 25 (H. H. K.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Newport, June 18 (D. B. Y.); Old Forge, August (J. G. N.).
Monroe County: Rochester Junction, June 1 (M. D. L.).
Oneida County: Lee Center, July 26 (W. A. C.).
Queens County: Flushing, June 22 (C. R. P.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 23 to August 12 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).

Subgenus *Hoplolabis* Osten Sacken

*Erioptera armata* O. S.

Erie County: Hamburg, May 14 to September 5 (M. C. VD.); East Aurora, May 18 (M. C. VD.); Buffalo, May 22 (M. C. VD.); Lancaster, June 19 to August 14 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9–13 (C. P. A.).
Monroe County: Rochester Junction, June 1 (M. D. L.).
Tompkins County: Ithaca, May 12–15 (C. P. A.); McLean, September 28 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Subgenus *Mesocyphona* Osten Sacken

*Erioptera caloptera* Say

Albany County: Helderbergs, July 3 (C. P. A.).
Cayuga County: North Fair Haven, September 14 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Gowanda, June 7 (M. C. VD.); Buffalo, June 23–25 (M. C. VD.); East Aurora, August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Queens County: Flushing, June 14 (C. R. P.).
Tompkins County: Ithaca, May 13 to June 19 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Erioptera* Meigen (*continued*)
Subgenus *Mesocyphona* Osten Sacken (*continued*)
*E. needhami* Alex.
Cortland County: Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 11–18 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca (R. H. T.).
*E. parva* O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Colden, August 7 (M. C. VD.).
Fulton County: Johnstown, September 15 (C. P. A.).
Tompkins County: Ithaca, August 2 (C. P. A.).
Subgenus *Empeda* Osten Sacken
*Erioptera nyctops* Alex.
Fulton County: Mountain Lake, June 13 (C. P. A.), T. L.; Mount Buell, June 18 (C. P. A.).
*E. stigmatica* (O. S.)
Albany County: Helderbergs, June 12 to July 3 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21–28 (M. C. VD.); East Aurora, June 1 (M. C. VD.); Lancaster, September 24 (M. C. VD.).
Fulton County: Sacandaga Park, June 5–24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, May 12 to June 20 (C. P. A.); McLean, September 28 (H. H. K.).

Genus *Molophilus* Curtis
*Molophilus forcipula* (O. S.)
Erie County: East Aurora, August 21 (M. C. VD.).
Fulton County: Gloversville, July 16 (C. P. A.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).
*M. fultonensis* Alex.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Mountain Lake, July 7 (C. P. A.), T. L.
*M. hirtipennis* (O. S.)
Albany County: Helderbergs, July 3 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Gowanda, June 8 (M. C. VD.); Elma, August 20 (M. C. VD.).
Fulton County: Johnstown, June 3–30 (C. P. A.); Mountain Lake, June 17 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, July and August (J. G. N.).
Oneida County: North Brook, June 22 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 29 to June 18 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*M. pubipennis* (O. S.)
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, June 19 (M. C. VD.); South Wales, July 9 (M. C. VD.).

Genus *Molophilus* Curtis (*continued*)
*M. pubipennis* (O. S.) (*continued*)
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Sacandaga Park, June 3 to August 11 (C. P. A.); etc.
Hamilton County: Wells, July 7–29 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).
Oneida County: Potash Creek, July 24 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 29 to July 13 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
*M. ursinus* (O. S.)
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Mayfield Mountain, June 21 to July 7 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).

Genus *Trimicra* Osten Sacken
*Trimicra anomala* O. S.
Erie County: Hamburg, May 28 (M. C. VD.); South Wales, July 9 (M. C. VD.).
Westchester County: New Rochelle (O. S.), T. L.

Genus *Helobia* St. Fargeau et Serville
*Helobia hybrida* (Meig.)
Albany County: Clinton Heights, April 9 (D. B. Y.); Karner, June 5 (D. B. Y.).
Erie County: Buffalo, March 4 to October 3 (M. C. VD.); Lancaster, May 9 (M. C. VD.); etc.
Fulton County: Johnstown, June 30 (C. P. A.); etc.
Hamilton County: Elm Lake, August 7 (D. B. Y.).
Herkimer County: Newport, June 18 (D. B. Y.); Old Forge, July 20–24 (J. G. N.).
Madison County: Canastota (J. C. F.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, March 25 to August 7 (C. P. A.); etc.

Genus *Gnophomyia* Osten Sacken
*Gnophomyia tristissima* O. S.
Albany County: Albany, September 11 (D. B. Y.).
Dutchess County: Poughkeepsie, June 8 (D. B. Y.).
Erie County: Gowanda, June 15 (M. C. VD.); Buffalo, June 25 to August 25 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 6 to August 24 (C. P. A.); Johnstown, September 20 (C. P. A.); etc.
Nassau County: Sea Cliff, September 3–5 (N. B.).
Niagara County: Niagara Falls, July 30 to October 9 (M. C. VD.).
Rensselaer County: Rensselaer, June 3 (D. B. Y.).
Suffolk County: O. S., in the type series at Cambridge.
Tompkins County: Ithaca, May 30 to June 10 (J. G. N.); Norton's Landing, June 19 (H. H. S.); etc.
Westchester County: Tarrytown, June 16–25 (S. W. F.).

Genus *Gonomyia* Meigen
Subgenus *Leiponeura* Skuse
*Gonomyia alexanderi* (Johns.)
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
*G. manca* (O. S.)
Fulton County: Sacandaga Park, August 26 (C. P. A.).

Genus *Gonomyia* Meigen (*continued*)
Subgenus *Leiponeura* Skuse (*continued*)
*G. sacandaga* Alex.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.), T. L.
Subgenus *Gonomyia* Meigen
*Gonomyia blanda* O. S.
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, July 19 (C. P. A.).
*G. cognatella* O. S.
Erie County: Gowanda, June 8 (M. C. VD.).
Fulton County: Sacandaga Park, June 18 to August 26 (C. P. A.).
Herkimer County: Indian Castle, June 10–13 (C. P. A.).
*G. florens* Alex.
Fulton County: Sacandaga Park, June 18 (C. P. A.); Gloversville, June 22 (C. P. A.).
Herkimer County: Indian Castle, June 9–13 (C. P. A.), T. L.
Tompkins County: McLean, June 5 (C. P. A.).
*G. mathesoni* Alex.
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 12–16 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, August 24 (C. P. A.).
*G. noveboracensis* Alex.
Fulton County: Sacandaga Park, June 11 (C. P. A.), T. L.
*G. subcinerea* O. S.
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 (D. B. Y.).
Erie County: Lancaster, June 4 (M. C. VD.); Hamburg, July 10 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June 3 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9–13 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Rensselaer County: Brookview, July 13 (M. M. A.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 13 to August 7 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*G. sulphurella* O. S.
Clinton County: Peru, June 10 (C. R. C.).
Erie County: Lancaster, June 2 to August 14 (M. C. VD.); Buffalo, June 25 (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff, August (N. B.).
Tompkins County: Ithaca, May 13 to August 24 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Rhabdomastix* Skuse
Subgenus *Sacandaga* Alexander
*Rhabdomastix flava* (Alex.)
Fulton County: Sacandaga Park, June 11–28 (C. P. A.), T. L.
Hamilton County: Wells, July 6 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.).

Genus *Cryptolabis* Osten Sacken

*Cryptolabis paradoxa* O. S.

Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 18 to July 27 (C. P. A.).
Oneida County: Brown Brook, July 13 (W. A. C.).
Tompkins County: Ithaca, June 19–21 (C. P. A.); Enfield Falls, July 12.

Genus *Cladura* Osten Sacken

*Cladura delicatula* Alex.

Fulton County: Mayfield Mountain, October 1 (C. P. A.).
Hamilton County: Middle Lake, Hope Township, September 12–13 (C. P. A.).

*C. flavoferruginea* O. S.

Erie County: East Aurora, September 20 (M. C. VD.); Lancaster, September 24 (M. C. VD.); Hamburg, September 25 to October 16 (M. C. VD.); North Evans, October 22 to November 4 (M. C. VD.); etc.
Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Mayfield Mountain, September 20 (C. P. A.).
Genesee County: Batavia, September 28 (H. H. K.).
Hamilton County: Middle Lake, Hope Township, September 12 (C. P. A.).
Herkimer County: Trenton Falls, September (O. S.), T. L.
Monroe County: Rochester, October 10 (M. C. VD.).
Nassau County: Sea Cliff (N. B.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).
Onondaga County: Manlius, October 1 (H. H. S.).
Putnam County: Highlands, October 3 (J. S.).
Tioga County: Owego, October 24 (H. H. K.).
Tompkins County: McLean, September 28 (C. R. C. and H. H. K.); Ithaca, October 3–15 (C. P. A.).

Genus *Chionea* Dalman

*Chionea gracilis* Alex.

Tompkins County: Ithaca, December 15, T. L.

*C. noveboracensis* Alex.

Tompkins County: Ithaca, Coy Glen, February 25 (R. C. S.), T. L.

*C. primitiva* Alex.

Cayuga County: Cascade, Owasco Lake, November 15 (S. C. B. and C. R. C.), T. L.

*C. valga* Harris

Cattaraugus County: Otto, March 18.
Erie County: Lancaster (M. C. VD.), on snow.
Onondaga County: Manlius, October 1 (H. H. S.).
Steuben County: Lake Keuka, December (C. R. C.).
Tompkins County: Ithaca, November 18 (R. H. P.); December 15 (W. A. R.).

Regional species: *Molophilus nova-caesariensis* Alex.

Tribe Limnophilini

Genus *Adelphomyia* Bergroth

*Adelphomyia americana* Alex.

Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Woodworth's Lake, August 22 (C. P. A.), T. L.; Johnstown, September 15–23 (C. P. A.); etc.
Hamilton County: Wells, July 29 (D. B. Y.).
Tompkins County: Ithaca, September 10 (C. P. A.).

Genus *Adelphomyia* Bergroth (*continued*)
*A. cayuga* Alex.
Tompkins County: Vanishing Brook, Ithaca, August 16 (C. P. A.), T. L.
*A. minuta* Alex.
Fulton County: Sacandaga Park, June 1–15 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 12–23 (C. P. A.), T. L.; McLean, June 5 (C. P. A.).

Genus *Limnophila* Macquart
Subgenus *Lasiomastix* Osten Sacken
*Limnophila macrocera* (Say)
Albany County: Karner, June 19 (D. B. Y.); Pine Hills, July 1 (D. B. Y.).
Cattaraugus County: Little Valley, July 18 to August 7 (M. C. VD.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, May 31 (M. C. VD.); Gowanda, June 14 (M. C. VD.); etc.
Franklin County: Axton, June (A. D. M.).
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.
Hamilton County: Wells, July 20 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Manlius, August 18 (H. H. S.).
Suffolk County: Yaphank, May 29.
Tompkins County: Ithaca, May 23–26 (C. P. A.); McLean, June 5 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
*L. subtenuicornis* (Alex.)
Tompkins County: McLean, May 31 (C. P. A.); Ithaca, June 4–13 (C. P. A.), T. L.
*L. tenuicornis* O. S.
Fulton County: Mountain Lake, June 17–19 (C. P. A.); Gloversville, June 24 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 20–29 (C. P. A.); McLean, June 5 (C. P. A.).
Subgenus *Idioptera* Macquart
*Limnophila fasciolata* O. S.
Albany County: Albany, June 17 (D. B. Y.).
Tompkins County: McLean, June 5 (C. P. A.).
Subgenus *Limnophila* Macquart
*Limnophila adusta* O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Lancaster, May 31 (M. C. VD.); Buffalo, June 10–12 (M. C. VD.); etc.
Essex County: Wilmington, August 24 (J. C. B.).
Fulton County: Mount Buell, June 5 to July 7 (C. P. A.); etc.
Genesee County: Batavia, August 6 (H. H. K.).
Onondaga County: Green Lake, June 8 (C. P. A.); Manlius, September 6 (H. H. S.).
Schenectady County: Schenectady, June 14 (A. O.).
Tompkins County: Ithaca, May 21 to June 5 (C. P. A.); etc.
*L. albipes* Leon.
Fulton County: Mountain Lake, altitude 1590 feet, July 7 (C. P. A.).
Westchester County: Tarrytown, June 16 (S. W. F.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)

*L. alleni* Johns.
Albany County: Karner, June 19 (D. B. Y.).
Fulton County: Gloversville, June 9–22 (C. P. A.).
Tompkins County: Ithaca, June 20 (A. H. M.); etc.

*L. areolata* O. S.
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 (D. B. Y.).
Cattaraugus County: Rock City, June 6 (J. C. B.).
Erie County: Gowanda, June 14 (M. C. VD.); Hamburg, June 18 (M. C. VD.); etc.
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Mountain Lake, June 3–29 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Old Forge, June 20 (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 20 to June 5 (C. P. A.); etc.

*L. brevifurca* O. S.
Erie County: Holland, May 21 (M. C. VD.); Colden, May 23 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–17 (C. P. A.); Gloversville, June 3–15 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: McLean, May 13 to June 5 (C. P. A.); Ithaca, May 14–21 (C. P. A.); etc.

*L. contempta* O. S.
Fulton County: Sacandaga Park, July 3 (C. P. A.).

*L. edwardi* Alex.
Fulton County: Gloversville, June 22 (C. P. A.), T. L.

*L. emmelina* Alex.
Fulton County: Mount Buell, altitude 1600 feet, June 18 (C. P. A.).

*L. fratria* O. S.
Erie County: East Aurora, May 18 (M. C. VD.). (Van Duzee, auct.)
(The type-locality for *L. fratria* was supposed by Osten Sacken to be New York State.)

*L. imbecilla* O. S.
Erie County: Gowanda, June 7–14 (M. C. VD.); Buffalo, June 12–15 (M. C. VD.).
Fulton County: Sacandaga Park, June 26 (C. P. A.).
Genesee County: Batavia, August 1 (H. H. K.).
Herkimer County: Trenton Falls (O. S.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).

*L. inornata* O. S.
Fulton County: Sacandaga Park, June 1–11 (C. P. A.).
Herkimer County: Old Forge, August (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Oswego County: Oswego, July 17.
Tompkins County: Ithaca, reared May 25 (C. P. A.).

*L. laricicola* Alex.
Fulton County: Canada Lake, June 20 (C. P. A.), T. L.

*L. lenta* O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)
*L. lenta* O. S. (*continued*)
Erie County: Hamburg, May 26 (M. C. VD.); South Wales, July 9 (M. C. VD.); etc.
Fulton County: Johnstown, June 26 to September 2 (C. P. A.); etc.
Hamilton County: Wells, July 29 (D. B. Y.); Dug Mountain, August 8 (D. B. Y.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Saratoga County: Corinth, June 23 (D. B. Y.).
Tompkins County: Ithaca, May 26 to August 12 (C. P. A.).
*L. lutea* Doane
Tompkins County: McLean, May 31 (F. K.).
*L. luteipennis* O. S.
Albany County: Karner, June 13 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Colden, May 23 (M. C. VD.); Hamburg, May 26 (M. C. VD.).
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Greene County: New Baltimore, September 17 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
Tompkins County: Ithaca, May 7 to June 5 (C. P. A.); etc.
*L. nigripleura* A. & L.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Mountain Lake, June 17 to August 13 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
Tompkins County: Ithaca, May 31 (R. H. T.); etc.
*L. niveitarsis* O. S.
Fulton County: Mount Buell, altitude 1400 feet, June 18–29 (C. P. A.).
Herkimer County: Old Forge, July 20 (J. G. N.).
*L. noveboracensis* Alex.
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.), T. L.; etc.
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, July 11–12 (C. P. A.).
*L. quadrata* O. S.
Albany County: Albany, June 7 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 22 to June 6 (M. C. VD.); Buffalo, June 15 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 5 to July 7 (C. P. A.); etc.
Genesee County: Batavia, June 6 (H. H. K.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 21–29 (C. P. A.), July 25 (H. Y.); McLean, June 5 (C. P. A.); Ringwood Hollow, July 14 (H. Y.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*L. recondita* O. S.
Albany County: Albany, June 15 (D. B. Y.).
Erie County: Buffalo, June 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)
*L. recondita* O. S. (*continued*)
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 26–29 (C. P. A.); McLean, June 5 (C. P. A.). (Osten Sacken's T. L. is New York State.)
*L. similis* Alex.
Fulton County: Johnstown, June 10–26 (C. P. A.), T. L.; Sacandaga Park, June 29 (C. P. A.).
Hamilton County: Wells, July 7 (D. B. Y.).
*L. stanwoodae* Alex.
Fulton County: Sacandaga Park, June 11 (C. P. A.), T. L.
*L. subcostata* (Alex.)
Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June 3–9 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 7–31 (C. P. A.), T. L.; etc.
*L. sylvia* Alex.
Fulton County: Mountain Lake, altitude 1590 feet, June 13 (C. P. A.), T. L.
*L. tenuipes* (Say)
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Colden, June 7 (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.).
Onondaga County: Manlius, September 6 (H. H. S.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 20 to August 12 (C. P. A.); McLean, June 5 (C. P. A.).
*L. toxoneura* O. S.
Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Mount Buell, June 13–29 (C. P. A.); Gloversville, June 14–24 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Rensselaer County: Brookview, July 9 (M. M. A.).
*L. ultima* O. S.
Albany County: Albany, May 15, October 4–7 (D. B. Y.).
Cattaraugus County: Olean, September 5 (C. R. C.).
Erie County: Colden, August 7 (M. C. VD.).
Fulton County: Woodworth's Lake, August 12 (C. P. A.); Gloversville, September 15–17 (C. P. A.).
Hamilton County: Middle Lake, Hope Township, September 12 (C. P. A.).
Monroe County: Rochester, October 10 (M. C. VD.).
Tompkins County: May 8, October 12 (C. P. A.).
Subgenus *Ephelia* Schiner
*Limnophila aprilina* O. S.
Albany County: Karner, June 15 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Ephelia* Schiner (*continued*)
*Limnophila aprilina* O. S. (*continued*)
Erie County: Gowanda, June 27 (M. C. VD.); South Wales, July 9 (M. C. VD.).
Fulton County: Mountain Lake, June 15 to July 7 (C. P. A.).
Hamilton County: Wells, July 29 (D. B. Y.).
Tompkins County: Ithaca, May 12–29 (C. P. A.).
*L. johnsoni* Alex.
Fulton County: Mount Buell, June 15 (C. P. A.); Mountain Lake, altitude 1600 feet, June 17 (C. P. A.), T. L.
Tompkins County: Coy Glen, Ithaca, May 23 (C. P. A.).
Subgenus *Dicranophragma* Osten Sacken
*Limnophila fuscovaria* O. S.
Albany County: Karner, June 13 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Hamburg, June 6–20 (M. C. VD.); Gowanda, June 7 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Hamilton County: Wells, July 23 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 17 to August 12 (C. P. A.); Norton's Landing, June 24 (H. H. S.).
Westchester County: Tarrytown, June 9 (S. W. F.).
Wyoming County: Portage, May 24 (H. H. K.).
Subgenus *Prionolabis* Osten Sacken
*Limnophila munda* O. S.
Cattaraugus County: Mix Creek Valley, June 11 (J. C. B.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Mount Buell, June 13–29 (C. P. A.); Gloversville, June 16 (C. P. A.); etc.
*L. rufibasis* O. S.
Albany County: Albany, May 26 to June 5 (D. B. Y.).
Clinton County: Peru, June 23 (C. R. C.).
Erie County: Holland, May 21 (M. C. VD.); Lancaster, May 31 (M. C. VD.); etc.
Fulton County: Gloversville, May 20 to June 3 (C. P. A.); Mount Buell, June 13–17 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Oneida County: Remsen, June 5 (W. A. C.).
Tompkins County: Ithaca, May 4–31 (C. P. A.); Norton's Landing, June 2 (H. H. S.); McLean, June 5 (C. P. A.).
Wyoming County: Portage, May 24 (H. H. K.).
*L. simplex* Alex.
Fulton County: Woodworth's Lake, June 17 (C. P. A.).
Subgenus *Dactylolabis* Osten Sacken
*Limnophila cubitalis* O. S.
Cattaraugus County: Rock City, June 6–10 (J. C. B. and H. H. K.).
Tompkins County: Ithaca, May 7–30 (C. P. A.); Taughannock Falls, May 19 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Dactylolabis* Osten Sacken (*continued*)
*L. montana* O. S.
Albany County: Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: Spring Brook, June 25 (M. C. VD.).
Fulton County: Mount Buell, June 13–18 (C. P. A.); etc.
Herkimer County: Little Falls, June 9 (C. P. A.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Tompkins County: Ithaca, May 5–24 (C. P. A.).

Genus *Epiphragma* Osten Sacken
*Epiphragma fascipennis* (Say)
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 19–25 (D. B. Y.).
Cattaraugus County: Rock City, June 6–7 (J. C. B. and H. H. K.); Vandalia, June 9 (C. R. C.).
Erie County: Colden, May 23 to June 7 (M. C. VD.); Buffalo, June 10–23 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1–21 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, June 20 (J. G. N.).
Nassau County: Sea Cliff (N. B.).
Oneida County: Cincinnati Creek, May 26 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 14–30 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*E. solatrix* (O. S.)
Nassau County: Sea Cliff, June (N. B.).

Genus *Ula* Haliday
*Ula elegans* O. S.
Fulton County: Pinnacle Mountain, September 16 (C. P. A.); etc.
Herkimer County: Old Forge, August (J. G. N.).
Tompkins County: Ithaca, May 13 to June 20 (C. P. A.).
*U. paupera* O. S.
Erie County: Holland, May 21 (M. C. VD.); East Aurora, June 22 to August 24 (M. C. VD.).
Fulton County: Johnstown, May 13 (C. P. A.); etc.
Tompkins County: Ithaca, May 13 (C. P. A.).

Genus *Ulomorpha* Osten Sacken
*Ulomorpha pilosella* (O. S.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 11 (M. C. VD.); South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.).
Fulton County: Gloversville, June 3–9 (C. P. A.); Mountain Lake, June 13–17 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.).
Oneida County: Cyrus Brook, July 10 (W. A. C.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, June 20 (L. W. C.).

Regional species: *Limnophila irrorata* Johns., *L. marchandi* Alex., *L. mundoides* Alex., *L. novae-angliae* Alex., *L. osborni* Alex., *L. poetica* O. S., *L. unica* O. S.

Tribe **Hexatomini**

Genus *Penthoptera* Schiner

*Penthoptera albitarsis* O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Hamburg, July 10 (M. C. VD.); Boston, July 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 27 (C. P. A.); Woodworth's Lake, July 19 (C. P. A.).
Tompkins County: Ithaca, July 11 to August 12 (C. P. A.), September 17 (J. G. N.).

Genus *Eriocera* Macquart

*Eriocera brachycera* O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Near Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Colden, July 25 (M. C. VD.).
Fulton County: Pinnacle Mountain, altitude 2000 feet, August 4 (C. P. A.).
Herkimer County: Old Forge, July 12–16 (J. G. N.).

*E. cinerea* Alex.

Fulton County: Woodworth's Lake, June 15 (C. P. A.).
Tompkins County: Ithaca, reared from larvae, May 16 (C. P. A.); Bear Creek, Freeville, May 16 (C. P. A.); Norton's Landing, May 25 (H. H. S.).

*E. fuliginosa* O. S.

Erie County: North Evans, May 25 to July 4 (M. C. VD.); Colden, May 31 (M. C. VD.); etc.
(Determined by Van Duzee; species not seen by writer.)

*E. fultonensis* Alex.

Fulton County: Sport Island, Sacandaga River, altitude 750 feet, June 15–27 (C. P. A.).
Tompkins County: Ithaca, reared May 30 to June 6 (J. T. L.), June 13 (C. P. A.), June 23 (H. Y.).

*E. longicornis* (Walk.)

Albany County: Albany, May 6 (D. B. Y.).
Erie County: North Evans, May 14 (M. C. VD.).
Fulton County: Fish-House, May 28 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.); Dolgeville, May 16 (C. P. A.).
Tompkins County: Ithaca, May 1–30 (C. P. A. and J. G. N.); etc.

*E. spinosa* (O. S.)

Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 5 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Oneida County: Tannery Brook, September 9 (larvae) (W. A. C.).
Tompkins County: Ithaca, May 17 to August 5; etc.

*E. tristis* Alex.

Tompkins County: Ithaca, August 1 (C. P. A. and C. I.), T. L.

Genus *Hexatoma* Latreille

*Hexatoma megacera* (O. S.)

Fulton County: Johnstown, May 24 (C. P. A.); Sport Island, Sacandaga River, June 15 (C. P. A.); etc.
Tompkins County: Ithaca, May 15 (C. P. A.); North Lansing, June 1 (S. C. B.); etc.

Regional species: *Eriocera wilsonii* O. S.

Tribe Pediciini

Genus *Pedicia* Latreille

*Pedicia albivitta* Walk.

Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.).
Broome County: Binghamton.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); East Aurora, August 15 to September 11 (M. C. VD.); etc.
Fulton County: Gloversville, June 11 (A. O.); Mountain Lake, August 22 (C. P. A.); etc.
Hamilton County: Middle Lake, September 12 (C. P. A.).
Herkimer County: Trenton Falls (O. S.).
Onondaga County: Manlius, August 27 (H. H. S.); Baldwinsville, September
Tompkins County: Ithaca, August 1–12 (C. P. A.); etc.
Ulster County: Big Indian Valley, May 24 to August 23 (R. F. P.)
Westchester County: Mosholu.

*P. contermina* Walk.

Tompkins County: McLean, May 13 (C. P. A.); Ithaca, June 1 (C. R P.); June 6 (S. A. G.).

Genus *Tricyphona* Zetterstedt

*Tricyphona auripennis* (O. S.)

Herkimer County: Indian Castle, June 10–13 (C. P. A.).

*T. autumnalis* Alex.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Grand Island, September 6 (M. C. VD.).
Essex County: Mount Marcy, July 30 (D. B. Y.).
Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Woodworth's Lake, September (C. P. A.), T. L.
Hamilton County: Elm Lake, August 2 (D. B. Y.); Dug Mountain, August 8 (D. B. Y.).

(Needham's record for *T. calcar*, Old Forge, August, probably belongs here.)

*T. calcar* (O. S.)

Cattaraugus County: Four-Mile, altitude 2300 feet, June 6 (J. C. B.).
Erie County: Colden, May 23 (M. C. VD.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Sacandaga Park, June 1; Gloversville, June 3 (C P. A.); etc.
Herkimer County: Newport, June 6 (D. B. Y.).
Tompkins County: McLean, May 22 to June 5 (C. P. A.); etc.

*T. inconstans* (O. S.)

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Columbia County: Claverack, September 28 (J. S.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Hamburg, May 31 to June 20 (M. C. VD.); Boston, September 3 (M. C. VD.); etc.
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Gloversville, June 10–27 (C. P. A.); Sacandaga Park, June 16 to August 24 (C. P. A.); etc.
Genesee County: Batavia, June 6 (H. H. K.).
Hamilton County: Mount Buell, June 13 (C. P. A.)

Genus *Tricyphona* Zetterstedt (*continued*)
*T. inconstans* (O. S.) (*continued*)
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.); Newport, August 31 (D. B. Y.).
Onondaga County: Manlius, September 10 (H. H. S.).
Monroe County: Rochester, October 10 (M. C. VD.).
Nassau County: Sea Cliff (N. B.).
Queens County: Rockaway Beach, June 26.
Schenectady County: Schenectady, June 14 (A. O.).
Tompkins County: Ithaca, May 12 to September 28 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
Wyoming County: Portage, May 24 (H. H. K.); Portageville, June 13 (C. R. C.).
*T. paludicola* Alex.
Tompkins County: McLean, May 13-20 (C. P. A. and P. W. C.), T. L.; Bear Creek, Freeville, May 16 (C. P. A.).
*T. vernalis* (O S.)
Fulton County: Mountain Lake, June 13-15 (C. P. A.); Mount Buell, June 15 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff, April (N. B.).
Tompkins County: Forest Home, May 7 (S. W. F.); Taughannock, May 8 (R. H. T.).

Genus *Dicranota* Zetterstedt
*Dicranota noveboracensis* Alex.
Fulton County: Dolgeville, May 16 (C. P. A.), T. L.
Tompkins County: Ithaca, April 24 (S. W. F.); May 8 (C. P. A.); etc.
*D. rivularis* O. S.
Tompkins County: Ithaca, April 21 (C. R. P.).

Genus *Rhaphidolabis* Osten Sacken
Subgenus *Rhaphidolabina* Alexander
*Rhaphidolabis flaveola* O. S.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.).
Fulton County: Gloversville, June 3–15 (C. P. A.); Mount Buell, June 13–17 (C. P. A.); Woodworth's Lake, August 22 (C. P. A.).
Hamilton County: Wells, July 9 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: Ithaca, May 30–31 (C. P. A.); etc.
Subgenus *Rhaphidolabis* Osten Sacken
*Rhaphidolabis cayuga* Alex.
Fulton County: Johnstown, August 19 (C. P. A.); Mountain Lake, September 2 (C. P. A.).
Tompkins County: Ithaca, April 22 (J. G. N.); McLean, May 13 (C. P. A.), T. L.
*R. rubescens* Alex.
Fulton County: Gloversville, altitude 900 feet, June 22 (C. P. A.), T. L.
*R. tenuipes* O. S.
Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: North Evans, May 14 (M. C. VD.); Holland, May 21 (M. C. VD.).

Genus *Rhaphidolabis* Osten Sacken (*continued*)
Subgenus *Rhaphidolabis* Osten Sacken (*continued*)
*R. tenuipes* O. S. (*continued*)
Fulton County: Gloversville, May 13 to August 5 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August 6 (J. G. N.).
Oneida County: Field's Brook, August 30 (W. A. C.).
Saratoga County: Saratoga Springs (O. S.), T. L.
Tompkins County: Ithaca, May 1 to August 12 (J. G. N.).
Subgenus *Plectromyia* Osten Sacken
*Rhaphidolabis modesta* (O. S.)
Erie County: Holland, May 21 (M. C. VD.). (Van Duzee, auct.)
Fulton County: Mountain Lake, altitude 1600 feet, June 13 (C. P. A.).

Regional species: *Dicranota eucera* O. S., *D. pallida* Alex., *Tricyphona hyperborea* (O. S.) *T. katahdin* Alex.

## Subfamily Cylindrotominae

Genus *Cylindrotoma* Macquart
*Cylindrotoma tarsalis* Johns.
Fulton County: Gloversville, June 9 (C. P. A.); Woodworth's Lake, altitude 1650 feet, June 17 to August 19 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).

Genus *Liogma* Osten Sacken
*Liogma nodicornis* (O. S.)
Erie County: Hamburg, May 28 to June 20 (M. C. VD.); Colden, June 7 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15–26 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: North Lansing, June 1 (C. R. C.); Ithaca, June 10–14 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Phalacrocera* Schiner
*Phalacrocera neoxena* Alex.
Cayuga County: North Fair Haven, May 17, dead in lake drift (J. G. N. and E. M.), T. L.
*P. tipulina* O. S.
Essex County: Lake Tear of the Clouds, Mount Marcy, July 10 (C. R. C.).
Fulton County: Near Sacandaga Park, June 18 (C. P. A.); Canada Lake, June 23 to July 10 (C. P. A.); etc.
Herkimer County: Old Forge, July, August 3 (J. G. N.).
Tompkins County: Ringwood Hollow, July 3 (H. Y.).

Regional species: *Cylindrotoma americana* O. S., *Triogma exculpta* O. S.

## Subfamily Tipulinae

### Tribe Dolichopezini

Genus *Dolichopeza* Curtis
*Dolichopeza americana* Needm.
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–15 (C. P. A.); Mountain Lake, June 13–17 (C. P. A.).

Genus *Dolichopeza* Curtis (*continued*)
*Dolichopeza americana* Needm. (*continued*)
Herkimer County: Old Forge, August (J. G. N.), T. L.
Queens County: Flushing, June 22 (C. R. P.).

Genus *Oropeza* Needham
*Oropeza albipes* Johns.
Cattaraugus County: Four-Mile, July 4 (H. H. K.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Colden, July 3 (M. C. VD.); South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 28 (C. P. A.).
Herkimer County: Old Forge, June 20 (J. G. N.).
Suffolk County: Bellport, August 9.
Westchester County: Tarrytown, June 9 (S. W. F.).
*O. obscura* Johns.
Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.); Four-Mile, July 4 (H. H. K.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 16 (M. C. VD.); South Wales, June 23 to July 9 (M. C. VD.).
Fulton County: Woodworth's Lake, June 15 to August 20 (C. P. A.); etc.
Hamilton County: Wells, July 30 (D. B. Y.).
Tompkins County: Ringwood Hollow, July 6 (H. Y.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).
*O. sayi* Johns.
Erie County: South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.).
Herkimer County: Old Forge, August (J. G. N.).
Niagara County: Niagara Falls, June 23.
Tompkins County: Ithaca, August (J. G. N.).
*O. similis* Johns.
Erie County: Gowanda, June 7–14 (M. C. VD.); Elma, August 20 (M. C. VD.).
*O. subalbipes* Johns.
Erie County: South Wales, July 9 (M. C. VD.).
Westchester County: Tarrytown, June 9 (S. W. F.)
*O. venosa* Johns.
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, June 23 (M. C. VD.).
Fulton County: Mountain Lake, June 15–17 (C. P. A.); Northampton, June 25 (D. B. Y.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: McLean, June 5 (C. P. A.).

Regional species: *Brachypremna dispellens* (Walk.), *Oropeza dorsalis* Johns.

Tribe **Ctenophorini**

Genus *Tanyptera* Latreille
*Tanyptera frontalis* (O. S.)
Cattaraugus County: Rock City, June 16 (J. C. B. and W. T. M. F.).
Fulton County: Mountain Lake, June 13 (C. P. A.).
Tompkins County: Ithaca, May 30–31 (C. I.).

Genus *Tanyptera* Latreille (*continued*)
*T. fumipennis* (O. S.)
Erie County: Colden, May 30 (M. C. VD.).
Tompkins County: Ithaca, May 30–31 (C. I.).
*T. topazina* (O. S.)
Erie County: Lancaster, May 31 (M. C. VD.).
Tompkins County: Ithaca, May 31.

Genus *Ctenophora* Meigen
*Ctenophora apicata* O. S.
Fulton County: Mount Buell, altitude 1400 feet, June 29 (C. P. A.).
Suffolk County: Long Island, July.

Tribe **Tipulini**

Genus *Longurio* Loew
*Longurio testaceus* Loew
Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Gloversville, altitude 1000 feet, June 27 (C. P. A.).
Nassau County: Sea Cliff (N. B.).

Genus *Stygeropis* Loew
*Stygeropis fuscipennis* Loew
Albany County: Albany, August 6 (D. B. Y.).
Erie County: East Aurora, June 11 (M. C. VD.).
Fulton County: Sacandaga Park, June 29 (C. P. A.); Mountain Lake, August 13 (C. P. A.).
Tompkins County: Ithaca, July 10 (C. P. A.); Ringwood Hollow, larvae in November and May (C. H. K.).

Genus *Nephrotoma* Meigen
*Nephrotoma breviorcornis* (Doane)
Fulton County: Sacandaga Park, June 29 (C. P. A.).
*N. calinota* (Dietz)
Fulton County: Sacandaga Park, June 19 (C. P. A.).
*N. eucera* (Loew)
Fulton County: Sacandaga Park, June 11–16 (C. P. A.).
Onondaga County: Manlius, June 12 (H. H. S.).
Suffolk County: Long Island.
Tompkins County: Ithaca, June 29 to July 21.
*N. ferruginea* (Fabr.)
Albany County: Albany, June 7 (D. B. Y.); Helderbergs, July 3 (C. P. A.).
Cortland County: Gee Brook, July 20 (A. O.); Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Buffalo, June 26 (J. G. N.); June 27 to November 11 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Genesee County: Batavia, September 3 (H. H. K.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Jefferson County: Alexandria Bay, September 3.
Monroe County: Honeoye Falls, July 4 to September 1 (C. R. C.).
Onondaga County: Baldwinsville, June 14; Manlius, August 18 (H. H. S.).
Ontario County: Clifton Springs, August 23.
Suffolk County: Astoria; Maspeth, June 1; Bellport, June 2; North Beach, September 18.
Sullivan County: White Lake, August 21 (J. L. Z.).
Tompkins County: Ithaca, May 7 to September 20 (C. P. A.); etc.

Genus *Nephrotoma* Meigen (*continued*)

*N. gracilicornis* (Loew)
Onondaga County: Manlius, August 8 (H. H. S.).

*N. incurva* (Loew)
Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 12 to August 25 (M. C. VD.); South Wales, July 9–13 (M. C. VD.).
Essex County: Keene Valley, July 26 (J. A. L.).
Fulton County: Sacandaga Park, June 1–11 (C. P. A.); etc.
Genesee County: Batavia, July 22 (H. H. K.).
Greene County: New Baltimore, May 29 (D. B. Y.).
Hamilton County: Lake Placid, August 7 (J. A. L.).
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Onondaga County: Manlius, August 24 (H. H. S.).
Tompkins County: Ithaca, June 18 to August 4 (C. P. A.); etc.

*N. lugens* (Loew)
Albany County: Karner, June 26 (D. B. Y.).
Cattaraugus County: Rock City, June 16 (H. H. K.).
Essex County: Elizabethtown, June 8 (D. B. Y.); Keene Valley, June 17 (J. A. L.).
Fulton County: Sacandaga Park, June 5-16 (C. P. A.); etc.
Genesee County: Batavia, July 19 (H. H. K.).
Herkimer County: Newport, May 29 (D. B. Y.); Indian Castle, June 13 (C.P. A.).
Steuben County: Lake Keuka, June 15 (C. R. C.).
Tompkins County: Ithaca, May 25 to June 29 (C. P. A.); Norton's Landing, June 2 (H. H. S.).

*N. macrocera* (Say)
Fulton County: Sacandaga Park, June 11–29 (C. P. A.); etc.
Westchester County: Tarrytown, June 16 (S. W. F.).

*N. pedunculata* (Loew)
Cattaraugus County: Four-Mile, July 4 (H. H. K.).
Cortland County: Taylor, July 20 (C. P. A.).
Essex County: Keene Valley, July 30 (J. A. L.).
Fulton County: Sacandaga Park, June 15 (C. P. A.).
Genesee County: Batavia, June 27 (H. H. K.).
Suffolk County: Long Island, July.

*N. polymera* (Loew)
Fulton County: Sacandaga Park, June 11–29 (C. P. A.).
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Rensselaer County: Brookview, July 16 (M. M. A.)
Tompkins County: Ithaca, June 29.

*N. sodalis* (Loew)
Onondaga County: Baldwinsville, June 13.

*N. tenuis* (Loew)
Cattaraugus County: Rock City, June 16 to July 4 (H. H. K.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Dutchess County: Poughkeepsie, June 4 (D. B. Y.).
Erie County: Colden, July 10 (M. C. VD.); East Aurora, July 23 to August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11–27 (C. P. A.); etc.
Genesee County: Batavia, June 22 (H. H. K.).
Sullivan County: August (Dietz collection).
Tompkins County: Ithaca, July 4 to August 2.
Westchester County: Tarrytown, June 16 (S. W. F.).

Genus *Nephrotoma* Meigen (*continued*):

*N. virescens* (Loew)

Fulton County: Mountain Lake, altitude 1500 feet, August 13 (C. P. A.).

Tompkins County: Cascadilla Creek, near Ithaca, July 11 (H. Y.).

*N. xanthostigma* (Loew)

Erie County: Colden, August 7 (M. C. VD.); Lancaster, September 13 (M. C. VD.); etc.

Suffolk County: Yaphank, June 28 (A. M. N.); Cold Spring Harbor, July 15 (A. L. M.); Bellport, August 1.

Sullivan County: August, 1912 (Dietz collection).

Genus *Tipula* Linnaeus

Subgenus *Cinctotipula* Alexander

*Tipula algonquin* Alex.

Essex County: Keene Valley, July 29 (J. A. L.); Elizabethtown, August 25 (D. B. Y.).

*T. unimaculata* (Loew)

Essex County: New Russia, August (J. C. B.)

Fulton County: Sacandaga Park, August 24 (C. P. A.).

Hamilton County: Hope Township, September 12–13 (C. P. A.).

Onondaga County: Manlius, September 6 (H. H. S.).

Tompkins County: Norton's Landing, September 6 (H. H. S.).

Wayne County: Sodus, August 15.

Subgenus *Odontotipula* Alexander

*Tipula unifasciata* (Loew)

Onondaga County: Manlius, August 29 (H. H. S.).

Tompkins County: Norton's Landing, August 12 (H. H. S.).

Subgenus *Trichotipula* Alexander

*Tipula oropezoides* Johns.

Erie County: Hamburg, May 28 (M. C. VD.).

Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June 6–28 (C. P. A.).

Herkimer County: Indian Castle, June 13 (C. P. A.).

Tompkins County: McLean, May 22 to June 5 (H. E. S.). Ithaca, May 29 to June 10 (C. P. A.).

Subgenus *Tipula* Linnaeus

*Tipula abdominalis* (Say)

Albany County: Coeymans, August 5.

Delaware County: Arkville, August (F. N. H.). (In Kansas University collection.)

Erie County: Gowanda, June 7–14, August 30 (M. C. VD.).

Essex County: Keene Valley, July 1 (J. A. L.); Lake Placid, August 19; New Russia, September 12–30 (J. C. B.).

Franklin County: Saranac Inn (J. G. N.).

Fulton County: Gloversville, July 29 to August 20 (Bromme).

Herkimer County: Old Forge, August 4 (J. G. N.).

Livingston County: Hemlock Lake, August 29 (C. R. C.).

Monroe County: Rochester Junction, June 9 (M. D. L.).

Oneida County: Brown Brook, July 14 (larvae) (W. A. C.).

Schoharie County: Sharon Springs (O. S.).

Suffolk County: Long Island, July.

Sullivan County: August (Dietz collection).

Tompkins County: Ithaca, August 30 to September 10.

Ulster County: Catskills, July (O. S.); Ellenville, August 10 (A. M. N.).

Wayne County: Newark, May 14.

Wyoming County: Portage, May 24 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)

*T. afflicta* Dietz
Erie County: South Wales, July 9 (M. C. VD.).

*T. angustipennis* Loew
Albany County: Karner, May 22 to June 13 (D. B. Y.); Albany, June 2 (D. B. Y.).
Erie County: Holland, May 21 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–11 (C. P. A.); etc.
Herkimer County: Ilion, May 17 (D. B. Y.); Indian Castle, June 13 (C. P. A.)
Tompkins County: Ithaca, April 26 to June 20 (C. P. A.); etc.

*T. apicalis* Loew
Albany County: Albany, June 26 (D. B. Y.).
Essex County: Keene Valley, July 13 (J. A. L.).
Fulton County: Sacandaga Park, June 5–16 (C. P. A.).
Tompkins County: Ithaca, May 24–29; McLean, May 31 to June 5 (C. P. A.)
Westchester County: Dobbs Ferry (O. S.), T. L.

*T. bella* Loew
Albany County: Albany, June 7 (D. B. Y.).
Broome County: Binghamton (Dietz collection).
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: North Evans, May 24 (M. C. VD.); East Aurora, August 2 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to September 28 (C. P. A.); etc.
Genesee County: Batavia, September 1 (H. H. K.).
Greene County: New Baltimore, August 16 (D. B. Y.).
Monroe County: Honeoye Falls, September 1 (C. R. C.).
Nassau County: Sea Cliff, May (N. B.).
Oneida County: Remsen, July 5 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Queens County: May 16 to July.
Suffolk County: Bellport.
Tioga County: Willseyville, May 25 (W. A. H.).
Tompkins County: Ithaca, May 1 to September 10 (C. P. A.); etc.

*T. bicornis* Forbes
Erie County: East Aurora, June 11–16 (M. C. VD.); Lancaster, June 19 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 29 (C. P. A.).
Orange County: West Point (O. S.).
St. Lawrence County: Potsdam, June.
Tompkins County: McLean, May 31 (C. P. A.); Ithaca, June 5–12; July 3 (H. Y.); etc.

*T. caloptera* Loew
Erie County: North Evans, May 14 to June 28 (M. C. VD.); Colden, May 23 (M. C. VD.); etc.
Fulton County: Gloversville, May 18 to June 30 (C. P. A.); Sacandaga Park, June 1 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Niagara County: Niagara Falls, June 23 (M. C. VD.).
Oneida County: Mill Creek, July 7 (W. A. C.).
Rensselaer County: Brookview, July 16 (M. M. A).
Suffolk County: Yaphank, June 28 to September 2 (A. M. N.); Bellport, September.
Tompkins County: Ithaca, May 5–30 (C. P. A.); McLean, June 5 (C. P. A.); etc.
Wyoming County: Wyoming, June 25 (H. H. K.).

enus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)

*T. cayuga* Alex.
Fulton County: Gloversville, June 9 (C. P. A.); T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, May 13–30 (C. P. A.).

*T. collaris* Say
Albany County: Albany, May 8 (D. B. Y.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: Colden, May 23 to July 1 (M. C. VD.); Gowanda, June 8 (M. C. VD.); etc.
Fulton County: Gloversville, June 9–24 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff, May 20 (N. B.).
Tompkins County: Ithaca, May 3 to June 20 (C. P. A. and L. W. C.); etc.

*T. cunctans* Say
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Hamburg, September 11 to October 25 (M. C. VD.); Buffalo, September 25 to October 2 (M. C. VD.); etc.
Genesee County: Batavia, September 12–28 (H. H. K.).
Jefferson County: Alexandria Bay, September 3.
Kings County: Flatbush, September 13.
Niagara County: Niagara Falls, September 17 (M. C. VD.); Grand Island, October 4 (M. C. VD.).
Ontario County: Clifton Springs, September 12.
Tioga County: Owego, October 24 (H. H. K.).
Tompkins County: McLean, September 28 (C. R. C.); Ithaca, October 4.

*T. dejecta* Walk.
Albany County: Karner, April 25 (D. B. Y.); Albany, May 3 (D. B. Y.).
Erie County: Hamburg, May 14–22 (M. C. VD.); Colden, May 23–29 (M. C. VD.).
Fulton County: Gloversville, May 14 (C. P. A.).
Nassau County: Sea Cliff, May 1 (N. B.).
Tompkins County: Ithaca, April 26 to May 31 (C. P. A.).

*T. eluta* Loew
Dutchess County: Rhinebeck, July 27 (C. R. C.).
Erie County: Lancaster, May 31 (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11–29 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 24 (E. T. W.); etc.
Ulster County: Ellenville, July 20 (A. M. N.).

*T. fragilis* Loew
Erie County: Lancaster, September 24 (M. C. VD.); Buffalo, October 3 (M. C. VD.); etc.
Essex County: Lake Placid, altitude 2000 feet (Johnson collection).
Fulton County: Gloversville, September 7–20 (C. P. A.); etc.
Greene County: New Baltimore, September 17 (D. B. Y.).
Hamilton County: Big Notch Mountain, Hope Township, September 12 (C. P. A.).
Tompkins County: Ithaca, September 29 to October 9 (C. P. A.); Taughannock Falls, October 25 (C. R. C.).

*T. fuliginosa* (Say)
Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Rock City, June 16 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
*T. fuliginosa* (Say) (*continued*)
Erie County: Lancaster, June 4 (M. C. VD.); East Aurora, June 11 (M. C. VD.); Colden, July 3 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 13–27 (C. P. A.).
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Livingston County: Conesus Lake, June 22 (H. H. K.).
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, June 20 to July 4 (C. P. A.).
Wyoming County: Portage, June 13–22 (H. H. K.).
*T. fultonensis* Alex.
Fulton County: Mount Buell, Sacandaga Park, altitude 1500 feet, June 15 (C. P. A.), T. L.
*T. georgiana* Alex.
Westchester County: New Rochelle (O. S.), T. L.
*T. grata* Loew
Erie County: Buffalo, August 5 (M. C. VD.).
Herkimer County: Old Forge, July 6 (J. G. N.).
Western New York: (O. S.), T. L.
*T. hebes* Loew
Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Erie County: Colden, August 3 (M. C. VD.); Hamburg, August 10 (M. C. VD.); East Aurora, August 21 (M. C. VD.).
Fulton County: Sacandaga Park, June 29 (C. P. A.); Johnstown, July 31 (C. P. A.).
Genesee County: Batavia, August 10 (H. H. K.).
Herkimer County: Old Forge, July 20 (J. G. N.).
Suffolk County: Cold Spring Harbor, July 15 (A. L. M.).
Tompkins County: Ithaca, August 2–26 (C. P. A.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.); Lake George, August 17 (J. L. Z.).
*T. helderbergensis* Alex.
Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.), T. L.
Hamilton County: Wells, July 31 (D. B. Y.).
*T. hermannia* Alex.
Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Essex County: Keene Valley, July 14 (J. A. L.); New Russia, August (J. C. B.).
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.
Greene County: New Baltimore, August 16 (D. B. Y.).
Hamilton County: Wells, July 30 to August 31 (D. B. Y.); Speculator, August 27 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).
Livingston County: Hemlock Lake, August 29 (C. R. C.).
Niagara County: Niagara Falls, June 28 (M. C. VD.).
Rockland County: Palisades (O. S.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, June 17 (J. G. N.); etc.
Ulster County: Catskills, July (O. S.).
Westchester County: Tarrytown, June 9 (S. W. F.).
*T. hirsuta* Doane
Fulton County: Mayfield Mountain, June 19 (C. P. A.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)

*T. ignobilis* Loew
Albany County: Helderbergs, July 3 (C. P. A.).
Tompkins County: Ithaca, reared from larvae, May 21–26 (C. P. A.).
Ulster County: Catskills, July (O. S.).

*T. iroquois* Alex.
Fulton County: Mountain Lake, June 13 (C. P. A.); Gloversville, June 24 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, May 3 to June 20 (C. P. A.); Ludlowville, May 4 (E. M.).
Wyoming County: Portage, May 24 (H. H. K.).

*T. latipennis* Loew
Erie County: Buffalo, June 26 (M. C. VD.); Grand Island, June 26 (M. C. VD.).
Fulton County: Sacandaga Park, July 3 (C. P. A.).
Genesee County: Batavia, August 1 (H. H. K.).
Niagara County: Grand Island, June 26 (M. C. VD.).
Rensselaer County: Brookview, July 15 (M. M. A.).

*T. longiventris* Loew
Cattaraugus County: Rock City, June 6 (W. T. M. F.).
Erie County: East Auburn, June 11 (M. C. VD.).
Fulton County: Sacandaga Park, July 29 (C. P. A.); Woodworth's Lake, August (C. P. A.).
Suffolk County: Bellport, May 27, July 6. (Part of the type material was collected in New York State by Edwards.)

*T. macrolabis* Loew
Albany County: Helderbergs, July 3 (C. P. A.).
Fulton County: Mount Buell, June 18–27 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).

*T. margarita* Alex.
Tompkins County: Ithaca, June 12 (C. P. A.), T. L.

*T. mingwe* Alex.
Fulton County: Sacandaga Park, August 24 (C. P. A.).
Genesee County: Batavia, July 22 (H. H. K.).
Hamilton County: Bennett Lake, Hope Township, September 12 (C. P. A.), T. L.
Onondaga County: Manlius, August 20 (H. H. S.).
Schoharie County: Sharon Springs (O. S.).
Tompkins County: Ithaca, August 1 (C. P. A.).
Wayne County: Sodus, July 9.

*T. monticola* Alex.
Cattaraugus County: Rock City, June 16 (H. H. K.).
Fulton County: Woodworth's Lake, June 18 (C. P. A.), T. L.; etc.
Hamilton County: Wells, July 23 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, June 3 (S. A. G.); McLean, June 5 (C. P. A.).

*T. nobilis* (Loew)
Albany County: Karner, June 19 (D. B. Y.).
Fulton County: Sacandaga Park, June 17 (C. P. A.); Woodworth's Lake, June 23 (C. P. A.).
Tompkins County: McLean, June 5 (C. P. A.).
Wyoming County: June 25 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)

*T. parshleyi* Alex.
Franklin County: Axton, June 12–22 (A. D. M. and C. O. H.).

*T. penobscot* Alex.
Fulton County: Mount Buell, altitude 1800 feet, June 18 (C. P. A.).

*T. perlongipes* Johns.
Fulton County: Canada Lake, altitude 1500 feet, June 20 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).

*T. rohweri* Doane
Erie County: East Aurora, May 18 (M. C. VD.); Elma, August 20 (M. C. VD.).
(Mr. Van Duzee records this species, but the record seems very doubtful to the writer since typical *rohweri* is western in its distribution.)

*T. sackeniana* Alex.
Tompkins County: Ithaca, August 26 (C. P. A.), T. L.

*T. sayi* Alex.
Cattaraugus County: Olean, September 5 (C. R. C.).
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Elma, August 20 (M. C. VD.); Hamburg, September 11–25 (M. C. VD.); Buffalo, September 21 (M. C. VD.); etc.
Fulton County: Gloversville, September 17–25 (C. P. A.); etc.
Genesee County: Batavia, September 11 (H. H. K.).
Herkimer County: Old Forge, August 23 (J. G. N.).
New York: August 5 to September 23.
Orange County: Goshen, September 7; West Point, September 8 (O. S.).
Sullivan County: August (Dietz collection).
Tompkins County: Ithaca, August 26–28 (C. P. A.); etc.
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).

*T. senega* Alex.
Albany County: Helderbergs, June 12 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); East Aurora, June 11 (M. C. VD.).
Fulton County: Mountain Lake, June 13–23 (C. P. A.); Mount Buell, June 15–29 (C. P. A.).
Tompkins County: Ithaca, May 7 to June 20 (L. W. C.); McLean, June 5 (C. P. A.).

*T. serta* Loew
Erie County: Holland, May 21 (M. C. VD.); Lancaster, May 31 (M. C. VD.); Buffalo, June 5 (M. C. VD.).
Fulton County: Gloversville, June 6–20 (C. P. A.); etc.
Tompkins County: Ithaca, May 31 to June 20 (C. P. A.); etc.

*T. strepens* Loew
Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 6–20 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Niagara County: Niagara Falls, June 24 (M. C. VD.).
Rockland County: Palisades (O. S.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tioga County: Willseyville, May 25 (W. A. H.).
Tompkins County: Ithaca, May 20–29 (C. P. A.); McLean, June 5 (C. P. A.).

*T. submaculata* Loew
Albany County: Albany, June 26 (D. B. Y.); Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Four-Mile, July 4 (H. H. K.).

enus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
*T. submaculata* Loew (*continued*)
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: North Evans, July 4 (M. C. VD.).
Fulton County: Sacandaga Park, June 20 to July 4 (C. P. A.); Gloversville, June 27 (C. P. A.); etc.
Genesee County: Batavia, July 14–25 (H. H. K.).
Saratoga County: Corinth, June 23 (D. B. Y.).
Tompkins County: Ithaca, June 20 (L. W. C.); etc.
(Part of the type material was collected in New York State.)
*T. sulphurea* Doane
Onondaga County: Green Lake, June 8 (C. P. A.).
*T. taughannock* Alex.
Albany County: Helderbergs, June 12 (C. P. A.).
Fulton County: Mount Buell, altitude 1800 feet, June 13 (W. P. A. and C. P. A.), T. L.
Tompkins County: Taughannock Falls, May 19 (C. P. A.).
*T. tephrocephala* Loew
Albany County: Karner, June 5 (D. B. Y.).
Fulton County: Sacandaga Park, June 16–28 (C. P. A.); etc.
Genesee County: Batavia, June 1 (H. H. K.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Rockland County: Palisades (O. S.), T. L.
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 16–29 (C. P. A.); McLean, June 5 (C. P. A.).
*T. tricolor* Fabr.
Columbia County: Niverville, August 24 (A. P. M.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Fulton County: Gloversville, August 18 to September 12 (C. P. A.); etc.
Genesee County: Batavia, June 19 (H. H. K.).
Herkimer County: Indian Castle, June 9–13 (C. P. A.); Trenton Falls, July (O. S.).
New York: (Hy. Edwards collection.)
Suffolk County: July.
Tompkins County: Ithaca, May 29 to August 28 (C. P. A.); etc.
*T. trivittata* Say
Albany County: Albany, June 11 (D. B. Y.); Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Mix Creek Valley, June 11 (J. C. B.).
Cortland County: Blodgett Mills, June 29 (A. O.).
Erie County: Lancaster, May 31 to June 2 (M. C. VD.); South Wales, July 9 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 (C. P. A.); etc.
Genesee County: Batavia, June 22–23 (H. H. K.).
Niagara County: Niagara Falls, June 24 (M. C. VD.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 17 to July 2 (C. P. A.); etc.
*T. ultima* Alex.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Delaware County: Delhi, September 21 (A. M.).
Erie County: Hamburg, September 11–25 (M. C. VD.); Lancaster, September 13 (M. C. VD.); etc.
Fulton County: Gloversville, September 15–20 (C. P. A.); etc.
Genesee County: Batavia, September 12–28 (H. H. K.).
Hamilton County: Middle Lake, Hope Township, September 13 (C. P. A.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
*T. ultima* Alex. (*continued*)
Kings County: Flatbush, September 28.
Suffolk County: North Beach, September 18.
Tompkins County: Ithaca, September 29 to October 10 (C. P. A.).
Westchester County: Peekskill, September 15 (Van Atta).
*T. umbrosa* Loew
Essex County: Keene Valley, August 10 (J. A. L.).
Fulton County: Sacandaga Park, June 24–29 (C. P. A.).
Hamilton County: Long Lake, August 9 (J. A. L.).
Herkimer County: Old Forge, July 25 (J. G. N.).
Tompkins County: Ithaca, July 20 (L. W. C.).
*T. valida* Loew
Albany County: Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Rock City, June 16 (H. H. K.).
Erie County: Lancaster, June 2–4 (M. C. VD.); North Evans, July 4 (M. C. VD.); etc.
Fulton County: Woodworth's Lake, May 30 to June 15 (C. P. A.); Sacandaga Park, June 1–21 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tompkins County: Ithaca, May 26 to June 20 (C. P. A.).
*T. vicina* Dietz
Erie County: Lancaster, May 31 (M. C. VD.), T. L.; Hamburg, June 7 (M. C. VD.).

Regional species: *Aeshnasoma rivertonensis* Johns., *Nephrotoma approximata* (Dietz), *N. cingulata* (Dietz), *N. festina* (Dietz), *N. hirsutula* (Dietz), *N. obliterata* (Dietz), *N. occipitalis* (Loew), *N. penumbra* Alex., *N. punctum* (Loew), *N. stigmatica* (Dietz), *N. temeraria* (Dietz), *N. vittula* (Loew), *N. wyalusingensis* (Dietz), *Tipula angulata* Loew, *T. annulicornis* Say, *T. aprilina* Alex., *T. centralis* Loew, *T. cincticornis* Doane, *T. conspicua* Dietz, *T. fraterna* Loew, *T. huron* Alex., *T. johnsoniana* Alex., *T. mainensis* Alex., *T. megaura* Doane, *T. morrisoni* Alex., *T. pachyrhinoides* Alex., *T. ternaria* Loew.

### *Distribution of the Tipulidae and related families by life zones*

North America may be divided into seven roughly parallel belts, or zones, termed life zones, which extend more or less completely across the continent and are distinguished from one another by peculiarities of their fauna and flora, by the annual precipitation, and by other characteristics. Beginning with the treeless Arctic-Alpine zone in northern Canada and passing southward, they comprise the Hudsonian, the Canadian, the Transition, the Upper Austral, the Lower Austral, and finally the Tropical zone, the last-named being found in the United States only in southern Florida and Texas.

These belts are by no means regularly parallel. In certain localities they run north or south at right angles to their usual course and encroach

n the adjacent zones. Thus the Canadian life zone of southern Canada nd the northern United States extends southward in the mountains s far as Georgia, the same faunal and floral conditions prevailing in the igh Alleghenies of Virginia and the Great Smoky Mountains of western orth Carolina as are found at much lower levels in the northern parts f the United States. By this it is seen that the same result is obtained y climbing these mountains as by a long journey from south to north, rise of a few feet in altitude being equivalent to many miles of latitude. imilarly there are extensions of the Upper Austral zone northward nto the Transition zone, these being produced by favorable conditions f warmth and moisture. In New York State is found an extensive ustral belt along the southern shores of Lake Ontario, altho the country ue southward is Transitional or even Canadian in its tendencies. Such olated islands are by no means infrequent.[4]

The crane-fly fauna seems to be fairly well distributed in these zones, nd in the following pages the various species are arranged in neir respective places. As has already been stated, crane-flies are otable lovers of rich vegetation, usually near running or standing water. Definite groups of crane-fly species may be expected to occur in certain oral communities, this relationship being often well marked. In cold anadian woods, such as are found in the Adirondacks and Catskills nd as isolated islands in the bogs and gorges thruout the State, definite lant associations are found, each of which supports an equally well-efined society of crane-flies. As a correlation and aid in checking these arious species, the plants that the writer believes to be characteristic f the different life zones are herewith included.

*The Boreal region*

*The Arctic-Alpine zone.*— "The Arctic or Arctic-Alpine zone lies bove the limit of tree growth and is characterized by such plants as ne arctic poppy, dwarf willow, and various saxifrages and gentians. . . .

[4] The following papers refer to this subject:
ray, William L. The development of the vegetation of New York State. New York State Coll. Forestry, Syracuse Univ., Tech. pub. 3:1–186 1915.
aton, Elon Howard. Life zones of New York State. *In* Birds of New York. New York State Museum, Memoir 12¹:19–42. 1910.
errian, C. Hart. The geographic distribution of life in North America. Smithsonian Inst., Ann. Rept. Bd. Regents 1891: 365–415. 1893.
errian, C. Hart. Life zones and crop zones of the United States, Part II. U. S. Dept. Agr., Div. Biol. Survey, Bul. 10 : 18–53. 1898
iller, Gerrit S., jr. Life zones of New York. *In* Preliminary list of the mammals of New York. New York State Museum, Bul. 6²⁹ : 280–292. 1899.

Within the United States the Arctic-Alpine zone is restricted to the ar above timber-line on the summits of high mountains." (Merriam 1898:18–19.)

The crane-flies in this zone are considered in connection with thos in the Hudsonian zone.

*The Hudsonian zone.*— "The Hudsonian zone comprises the northe part of the great transcontinental coniferous forest — a forest of spruce and firs stretching from Labrador to Alaska — and . . . In the easte United States the Hudsonian zone is restricted to the cold summits the highest mountains, where it occurs in the form of a chain of widel separated islands reaching from northern New England to western Nort Carolina." (Merriam, 1898:19.)

The following plants may be considered as Hudsonian species:

*Hierochloë alpina* (Sw.) R. & S.
*Poa laxa* Haenke
*Scirpus caespitosus* L.
*Carex capillaris* L.
*rariflora* Smith
*rigida* Good.
*capitata* L.
*Juncus trifidus* L.
*Salix herbacea* L.
*Uva-ursi* Pursh
*Betula glandulosa* Michx.
*Arenaria groenlandica* (Retz.) Spreng.
*Saxifraga aizoides* L.
*Ranunculus lapponicus* L.
*Empetrum nigrum* L.
*Rhododendron lapponicum* (L.) Wahlenb.
*Cassiope hypnoides* (L.) D. Don.
*Arctostaphylos alpina* (L.) Spreng.
*Vaccinium caespitosum* Michx.
*uliginosum* L.
*Vitis-Idaea* L., var. *minus* Lod
*Diapensia lapponica* L.
*Primula mistassinica* Michx.
*Pinguicula vulgaris* L.
*Prenanthes nana* (Bigel.) Torr.
*Solidago Cutleri* Fernald

The following species of crane-flies may be considered as Arctic-Alpin species finding their southern limit in the Hudsonian zone:

*Rhabdomastix caudata* (Lundb.)
*Tricyphona hannai* Alex.
*hyperborea* (O. S.)
*Tipula aperta* Alex.
*appendiculata* Loew
*arctica* Curt.
*balioptera* Loew
*besselsi* O. S.
*canadensis* Loew
*Tipula centralis* Loew
*labradorica* Alex.
*loewiana* Alex.
*piliceps* Alex.
*septentrionalis* Loew
*serrulata* Loew
*subfasciata* Loew
*ternaria* Loew

*The Canadian zone.*— "The Canadian zone comprises the souther part of the great transcontinental coniferous forest of Canada, the norther parts of Maine, New Hampshire, and Michigan, . . . and the greate part of the high mountains of the United States and Mexico." (Merriam 1898:19.)

The following plants may be considered as Canadian species:

*Carex exilis* Dewey
*canescens* Waldenb.
*disperma* Schrank
*pauciflora* Lightf.
*leptalea* Wahlenb.
*Scirpus* (Wahlenb.) Willd.
*oligosperma* Michx.
*Salix calcicola* L.
*Chiastonia borealis* (Ait.) Raf.
*Smilacina stellata* (L.) Desf.
*Streptopus amplexifolius* (L.) DC.
*Trillium undulatum* Willd.
*Habenaria macrophylla* Goldie
*hookeri* (Willd.) R. Br.
*Asarum hirtum* L.
*Calypso bulbosa* (L.) Oakes
*Salix rostrata* Richards.
*serotina* Flügge
*Populus tremuloides* L.
*Betula alba* var. *papyrifera* (Marsh.) Spach.
*Stellaria borealis* Bigel.
*Cornus trifolia* (L.) Raf.
*Actaea rubra* (Ait.) Willd.
*Mitella nuda* L.
*Ribes triste* Pall.
*Pyrus americana* (Marsh.) DC.
*Potentilla tridentata* Ait.
*Dalibarda repens* L.
*Oxalis Acetosella* L.
*Ilex montana* Gray
*Acer spicatum* Lam.
*Rhamnus alnifolia* L'Hér.
*Viola Selkirkii* Pursh
*incognita* L.
*Epilobium molle* Torr.
*Circaea alpina* L.
*Panax quinquefolium* L.
*Cornus canadensis* L.
*Ledum groenlandicum* Oeder
*Kalmia polifolia* Wang.
*Andromeda glaucophylla* Link.
*Chamaedaphne calyculata* (L.) Moench
*Arctostaphylos Uva-ursi* (L.) Spreng.
*Clintonia borealis* (L.) T. & G.
*Maianthemum trifoliatum* L.
*Gaylussacia baccata* Wiegand
*Lonicera oblongifolia* (Goldie) Hook.
*Linnaea borealis* L., var. *americana* (Forbes) Rehder
*Viburnum alnifolium* Marsh.
*Solidago macrophylla* Pursh
*alpestris* Nutt.
*Senecio Robbinsii* Oakes

The following species of crane-flies may be considered as Canadian species:

*Rhipidia fenestralis* (Johns.)
*Dactylolabis halterata* O. S.
*Limnobia bathamiae* O. S.
*parvulina* O. S.
*willistoni* O. S.
*tristigma* O. S.
*Dactylolabis parmata* O. S.
*Pseudolimnophila maculipennis* (O. S.)
*Erioptera chrysocoma* O. S.
*nearctica* Alex.
*aperta* Alex.
*alpestris* (O. S.)
*arcuata* O. S.
*Ormosia mutabilis* (O. S.)
*pagana* (Alex.)
*Adelphomyia nigra* Alex.
*minuta* Alex.
*Limnophila adusta* Johns.
*johnsoni* Alex.
*acuta* O. S.
*arborea* Alex.
*stenocornis* Alex.
*subcostalis* (Alex.)
*subhamata* (Alex.)
*Limnophila tenuicornis* O. S.
*tuxedana* O. S.
*unica* O. S.
*Erioptera brachycera* O. S.
*Rhaphidolabis flavida* O. S.
*modesta* (O. S.)
*rubescens* Alex.
*Dicranota pallida* Alex.
*Trimicra curipennis* (O. S.)
*calcar* (O. S.)
*katahdin* Alex.
*Cylindrotoma americana* O. S.
*tarsalis* Johns.
*Phalacrocera occulta* Alex.
*lipulina* O. S.
*Nephrotoma perumbra* Alex.
*vittula* (Loew)
*Tipula angulata* Loew
*cayuga* Alex.
*macradenia* Loew
*mainensis* Alex.
*monticola* Alex.
*penobscot* Alex.
*serta* Loew

*The Canadian-Transition zone.*— A great many species occur in both the Canadian and the Transition life zone, and these for the most part find their northern or southern limit in one or the other of these belts. The floral constituents of this border zone are numerous and varied, a large number of the Canadian forms finding their southern limit in the Transition zone, and, conversely, many of the more southern species extending their range into, and finding their northern limit in favorable situations in, the Canadian zone. The more notable plants that seem to fall within this category are:

*Maianthemum canadense* Desf.
*Streptopus roseus* Michx.
*Medeola virginiana* L.
*Cypripedium arietinum* R. Br.
*hirsutum* Mill.
*Habenaria lacera* (Michx.) R. Br
*Laportea canadensis* (L.) Gaud.
*Arceuthobium pusillum* Peck
*Asarum canadense* L.
*Polygonum amphibium* L.
*Caltha palustris* L.
*Actaea alba* (L.) Mill.
*Caulophyllum thalictroides* (L.) Michx.
*Corydalis sempervirens* (L.) Pers.
*Pyrus arbutifolia* (L.) L. f.
*melanocarpa* (Michx.) Willd.
*Potentilla palustris* (L.) Scop.
*Rubus hispidus* L.
*Sanguisorba canadensis* L.
*Nemopanthus mucronata* (L.) Trel.
*Acer pennsylvanicum* L.
*Hypericum canadense* L.
*Trientalis americana* (Pers.) Pursh
*Gentiana linearis* Froel.
*Diervilla Lonicera* Mill.
*Viburnum cassinoides* L.
*Lobelia Kalmii* L.
*Solidago latifolia* L.
*rugosa* Mill.
*graminifolia* (L.) Salisb.
*Aster umbellatus* Mill.
*Anaphalis margaritacea* (L.) B. & H.
*Erechtites hieracifolia* (L.) Raf.

The majority of the crane-flies of the northeastern United States seem to belong here. There are many species which are strongly Canadian in their associations but still seem to range outside the Canadian zone. In the following list these species are designated by the letter *C*, in parenthesis. It must be understood that many of these species are about as typically Canadian as those given in the preceding list, but slight extensions of their range make it appear more desirable to include them in this qualified list.

The few species which are Transitional but range into the Canadian zone are here designated by the letter *T*.

*Protoplasa fitchii* O. S.
*Trichocera subsinuata* Alex. (C)
*Rhyphus alternatus* Say
*Dicranomyia gladiator* O. S. (C)
*globithorax* O. S. (C)
*haeretica* O. S.
*immodesta* O. S.
*Dicranomyia macateei* Alex. (C)
*monticola* (Alex.) (C)
*morioides* O. S.
*pubipennis* O. S. (C)
*pudica* O. S.
*Limnobia triocellata* O. S.
*Rhipidia fidelis* O. S.

*Rhipidia maculata* Meig.
*Atarba picticornis* O. S.
*Elephantomyia westwoodi* O. S. (C)
*Rhamphidia mainensis* Alex.
*Ormosia apicalis* Alex. (C)
*holotricha* (O. S.)
*innocens* (O. S.)
*meigenii* (O. S.)
*nigripila* (O. S.)
*nubila* (O. S.)
*rubella* (O. S.)
*Erioptera armata* O. S.
*armillaris* O. S.
*villosa* O. S. (C)
*Molophilus fultonensis* Alex. (C)
*hirtipennis* (O. S.)
*pubipennis* (O. S.)
*ursinus* (O. S.)
*Gnophomyia tristissima* O. S.
*Gonomyia alexanderi* (Johns.)
*blanda* O. S. (C)
*cognatella* O. S. (T)
*florens* Alex. (C)
*mathesoni* Alex.
*noveboracensis* Alex. (T)
*sacandaga* Alex. (T)
*subcinerea* O. S.
*sulphurella* O. S. (T)
*Rhabdomastix flava* (Alex.) (T)
*Cryptolabis paradoxa* O. S.
*Chionea valga* Harr.
*Cladura delicatula* Alex. (C)
*flavoferruginea* O. S.
*Adelphomyia americana* Alex. (C)
*Limnophila albipes* Leon. (C)
*aprilina* O. S. (C)
*areolata* O. S. (C)
*brevifurca* O. S. (C)
*edwardi* Alex. (C)
*emmelina* Alex. (C)
*fuscovaria* O. S. (C)
*imbecilla* O. S.
*inornata* O. S.
*laricicola* Alex. (C)
*lenta* O. S.
*montana* O. S.
*mundoides* Alex.
*nigripleura* A. & L. (C)
*niveitarsis* O. S. (C)
*noveboracensis* Alex. (C)
*quadrata* O. S.
*rufibasis* O. S. (C)
*sylvia* Alex. (C)
*ultima* O. S. (C)
*Ula elegans* O. S. (C)
*Ulomorpha pilosella* (O. S.) (C)
*Eriocera fultonensis* Alex.
*longicornis* (Walk.)
*spinosa* (O. S.)
*tristis* Alex.
*Hexatoma megacera* (O. S.)
*Dicranota eucera* O. S.
*noveboracensis* Alex.
*rivularis* O. S.
*Rhaphidolabis cayuga* Alex.
*tenuipes* O. S.
*Pedicia albivitta* Walk.
*contermina* Walk. (C)
*Tricyphona paludicola* Alex.
*vernalis* (O. S.) (C)
*Liogma nodicornis* (O. S.) (C)
*Triogma exculpta* O. S.
*Dolichopeza americana* Needm. (C)
*Oropeza albipes* Johns.
*obscura* Johns. (C)
*venosa* Johns. (C)
*Ctenophora apicata* O. S.
*Nephrotoma eucera* (Loew)
*incurva* (Loew)
*lugens* (Loew) (C)
*pedunculata* (Loew) (C)
*polymera* (Loew)
*tenuis* (Loew)
*xanthostigma* (Loew)
*Stygeropis fuscipennis* Loew
*Longurio testaceus* Loew (C)
*Tipula algonquin* Alex.
*angustipennis* Loew (C)
*apicalis* Loew (C)
*bicornis* Forbes
*caloptera* Loew
*collaris* Say (C)
*cunctans* Say (T)
*dejecta* Walk. (C)
*fragilis* Loew (C)
*fuliginosa* (Say) (T)
*hebes* Loew (C)
*hermannia* Alex. (C)
*hirsuta* Doane
*iroquois* Alex. (C)
*latipennis* Loew (C)
*longiventris* Loew
*megaura* Doane (C)
*mingwe* Alex.
*nobilis* (Loew) (C)
*oropezoides* Johns. (C)
*parshleyi* Alex. (C)
*perlongipes* Johns. (T)
*senega* Alex.

*Tipula strepens* Loew
*submaculata* Loew
*sulphurea* Doane (C)
*taughannock* Alex. (C)
*Tipula tephrocephala* Loew
*ultima* Alex. (T)
*unimaculata* (Loew)
*valida* Loew (C)

*The Austral region*

*The Transition zone.*—"The Transition zone . . . is the transcontinental belt in which Boreal and Austral elements overlap. From New England to the northern Rocky Mountains its course is fairly even and regular." (Merriam, 1898:20.)

The following plants may be considered as Transition species:

*Schizaea pusilla* Pursh
*Chamaecyparis thyoides* (L.) BSP.
*Trillium grandiflorum* (Michx.) Salisb.
*cernuum* L.
*Aletris farinosa* L.
*Smilax hispida* Muhl.
*Juglans nigra* L.
*Ulmus racemosa* Thomas
*Sassafras variifolium* (Salisb.) Ktze.
*Crotalaria sagittalis* L.
*Polygala Nuttallii* T. & G.
*Nyssa aquatica* L.
*Asclepias verticillata* L.
*Datura Stramonium* L.
*Pentstemon hirsutus* (L.) Willd.
*Dianthera americana* L.

The crane-flies of this area include the following species:

*Dicranomyia rara* O. S.
*Limnobia fallax* Johns.
*Dicranoptycha sobrina* O. S.
*Gonomyia manca* (O. S.)
*Limnophila cubitalis* O. S.
*fasciolata* O. S.
*irrorata* Johns.
*Aeshnasoma rivertonensis* Johns.
*Tipula annulicornis* Say
*eluta* Loew
*fraterna* Loew
*georgiana* Alex.
*sayi* Alex.
*tricolor* Fabr.
*tuscarora* Alex.
*umbrosa* Loew

*Limnophila cubitalis* perhaps might be better included in the list preceding this. *Tipula umbrosa* ranges from the Austral to the Canadian zone, but seems most numerous in the Transition zone.

*The Upper Austral zone.*—"The Carolinian faunal area [of the Upper Austral zone] . . . . occupies the larger part of the Middle States, except the mountains." (Merriam, 1898:30.)

The following plants may be considered as Upper Austral species:

*Pinus virginiana* Mill.
*echinata* Mill.
*Commelina communis* L.
*Saururus cernuus* L.
*Quercus falcata* Michx.
*marilandica* Muench.
*phellos* L.
*Nelumbo lutea* (Willd.) Pers.
*Cabomba caroliniana* Gray
*Asimina triloba* Dunal
*Corydalis flavula* (Raf.) DC.
*Liquidambar Styraciflua* L.
*Desmodium laevigatum* (Nutt.) DC.
*Lespedeza repens* (L.) Bart.
*Ptelea trifoliata* L.[5]
*Evonymus americanus* L.

[5] Species characteristic of this zone but running into the Transition zone.

*Ascyrum stans* Michx.
*Aralia spinosa* L.
*Ipomoea pandurata* (L.) G. F. W. Mey.
*Paulownia tomentosa* (Thunb.) Steud.
*Lonicera sempervirens* L.
*Viburnum nudum* L.

The following species of crane-flies belong to this zone:

*Dicranoptycha minima* Alex.
*nigripes* O. S.
*tigrina* Alex.
*winnemana* Alex.
*Toxorhina magna* (O. S.)[6]
*Gnophomyia luctuosa* O. S.[6]
*Epiphragma solatrix* (O. S.)
*Eriocera aurata* Doane
*wilsonii* O. S.
*Brachypremna dispellens* (Walk.)[6]
*Nephrotoma okefenoke* (Alex.)
*virescens* (Loew)[7]
*Tipula australis* Doane
*dietziana* Alex.
*flavibasis* Alex.
*morrisoni* Alex.

*The Lower Austral zone.*— "The Lower Austral zone occupies the southern part of the United States, from Chesapeake Bay to the great interior valley of California." (Merriam, 1898:41.)

This is a region characterized by a great number of southern plants, of which the cabbage palmetto (*Sabal palmetto* Lodd.), the Venus's fly-trap (*Dionaea muscipula* Ellis), and the crape myrtle (*Lagerstroemia indica* L.) may be cited as typical. The following species of crane-flies belong to this zone:

*Dicranomyia distans* O. S.
*floridana* O. S.
*Diotrepha mirabilis* O. S.[8]
*Gonomyia pleuralis* (Will.)[8]
*puer* Alex.[8]
*slossonae* Alex.[8]
*Polymera georgiae* Alex.
*Tipula aspidoptera* Alex.
*comanche* Alex.
*costaloides* Alex.
*guasa* Alex.
*ludoviciana* Alex.
*seminole* Alex.
*texensis* Alex.

*The Tropical region*

*The Tropical zone.*— "The Tropical region within the United States is of small extent and is restricted to three widely separated localities — southern Florida, extreme southeast Texas . . . , and the valley of the lower Colorado River in Arizona and California. The Florida area is genuine humid tropical." (Merriam, 1898:51–52.)

The following species of crane-flies pertain to this zone:

*Dicranomyia reticulata* Alex.
*Rhipidia schwarzi* Alex.
*Geranomyia virescens* Loew
*Erioptera immaculata* Alex.
*Megistocera longipennis* (Macq.)

[6] Southern species reaching their northern limit in this zone.
[7] Species characteristic of this zone but running into the Transition zone.
[8] Tropical species reaching their northern limit in this zone.

## SEASONAL DISTRIBUTION

Like many other groups of insects, the Holarctic crane-flies have a remarkably constant seasonal distribution, there being vernal, early summer, midsummer, and autumnal species, as well as forms that range over a much longer period. The vernal species appear soon after the melting of the ice in spring, and are on the wing for a month or two. Some few of these species reappear in late summer, and these are presumably double-brooded species. In New York, New England, and southern Canada the great majority of crane-flies are on the wing during the month of June. Among these are represented the last of the vernal forms and the first of the extensive midsummer fauna. In late summer a few additional species appear, and these are closely followed in September and October by about the same number of autumnal forms. The winter crane-flies, so-called, include species of Trichocera and Chionea which appear at other seasons of the year as well but are more easily detected during the mild, sunny days of winter.

In general it may be stated that the crane-flies of eastern America which fly in spring and summer come out later and disappear earlier in the northern part of their range — New York, New England, and southern Canada — than in the southern part — the Middle Atlantic and Southern States. The late summer and the autumnal species, however, come out earlier in the former regions than they do farther south, and disappear correspondingly early in the season, their period being restricted by the date of the first killing frost.

The dates as here given apply to the Transition areas of New York and New England. They should be considered as earlier in the vicinity of Washington — from one to three weeks or even more, depending on the situation — and later as one goes northward, with the exceptions given above. It must be understood and expected that considerable deviation from these dates and figures will be found, but it is believed that in most cases they are fairly accurate, being based on a vast number of records extending over many years.

The following are early to late spring species — from April 1 thru May, disappearing about the first of June but many of them reappearing in August and September. Most of these species appear for the first time about April 20. Helobia appears much earlier, in March or even in February. The species of Ormosia, Dicranota, and Rhaphidolabis are

especially characteristic of the early spring fauna, appearing in small swarms soon after the breaking up of the winter's snow and ice. Practically all the species have disappeared by June 1, but *Tipula trivittata* is found thruout the summer.

*Ormosia innocens* (O. S.)
*meigenii* (O. S.)
*nubila* (O. S.)
*Helobia hybrida* (Meig.)
*Limnophila subcostata* (Alex.)
*Dicranota eucera* O. S.
*noveboracensis* Alex.
*rivularis* O. S.
*Rhaphidolabis cayuga* Alex.
*Rhaphidolabis tenuipes* O. S.
*Pedicia contermina* Walk.
*Tricyphona paludicola* Alex.
*Tipula angustipennis* Loew
*collaris* Say
*dejecta* Walk.
*iroquois* Alex.
*tephrocephala* Loew
*trivittata* Say

In Europe the following species appear to be characteristic early spring forms:

*Tipula macrocera* Zett.
*maxima* Poda
*pabulina* Meig.
*Tipula variipennis* Meig.
*vittata* Meig.

Late spring to midsummer species — June, some persisting into July and a few reappearing in late summer — are as follows. *Limnophila brevifurca* appears in early May but is not common until June. It will be seen from this list that the majority of the local Limnophilas appear in the month of June.

*Protoplasa fitchii* O. S.
*Toxorhina muliebris* (O. S.)
*Dicranoptycha germana* O. S.
*Atarba picticornis* O. S.
*Rhamphidia mainensis* Alex.
*Erioptera nyctops* Alex.
*vespertina* O. S.
*Gnophomyia tristissima* O. S.
*Gonomyia florens* Alex.
*mathesoni* Alex.
*noveboracensis* Alex.
*subcinerea* O. S.
*sulphurella* O. S.
*Limnophila alleni* Johns.
*aprilina* O. S.
*areolata* O. S.
*brevifurca* O. S.
*cubitalis* O. S.
*edwardi* Alex.
*emmelina* Alex.
*fasciolata* O. S.
*fuscovaria* O. S.
*Limnophila johnsoni* Alex.
*munda* O. S.
*niveitarsis* O. S.
*poetica* O. S.
*quadrata* O. S.
*rufibasis* O. S.
*sylvia* Alex.
*tenuicornis* O. S.
*toxoneura* O. S.
*unica* O. S.
*Adelphomyia minuta* Alex.
*Ulomorpha pilosella* (O. S.)
*Hexatoma megacera* (O. S.)
*Eriocera cinerea* Alex.
*longicornis* (Walk.)
*spinosa* (O. S.)
*Tricyphona auripennis* (O. S.)
*calcar* (O. S.)
*vernalis* (O. S.)
*Rhaphidolabis flaveola* O. S.
*modesta* (O. S.)
*rubescens* Alex.

*Liogma nodicornis* (O. S.)
*Dolichopeza americana* Needm.
*Nephrotoma lugens* (Loew)
*Tipula apicalis* Loew
*cayuga* Alex.
*macrolabis* Loew
*monticola* Alex.
*Tipula oropezoides* Johns.
*penobscot* Alex.
*senega* Alex.
*serta* Loew
*submaculata* Loew
*sulphurea* Doane
*taughannock* Alex.

Early summer to midsummer species — from June 21 to August 10 — are as follows:

*Bittacomorphella jonesi* (Johns.)
*Dicranomyia globithorax* O. S.
*macateei* Alex.
*pubipennis* O. S.
*Limnobia triocellata* O. S.
*tristigma* O. S.
*Elephantomyia westwoodi* O. S.
*Ormosia monticola* (O. S.)
*nigripila* (O. S.)
*rubella* (O. S.)
*Erioptera armillaris* O. S.
*chlorophylla* O. S.
*chrysocoma* O. S.
*graphica* O. S.
*straminea* O. S.
*Molophilus fultonensis* Alex.
*hirtipennis* (O. S.)
*pubipennis* (O. S.)
*ursinus* (O. S.)
*Gonomyia alexanderi* (Johns.)
*blanda* O. S.
*manca* (O. S.)
*sacandaga* Alex.
*Rhabdomastix flava* (Alex.)
*Cryptolabis paradoxa* O. S.
*Limnophila albipes* Leon.
*inornata* O. S.
*nigripleura* A. & L.
*noveboracensis* Alex.
*stanwoodae* Alex.
*Penthoptera albitarsis* O. S.
*Eriocera fultonensis* Alex.
*tristis* Alex.
*Cylindrotoma americana* O. S.
*tarsalis* Johns.
*Phalacrocera neoxena* Alex.
*tipulina* O. S.
*Longurio testaceus* Loew
*Nephrotoma eucera* (Loew)
*xanthostigma* (Loew)
*Tipula fuliginosa* (Say)
*hebes* Loew
*hermannia* Alex.
*tricolor* Fabr.
*valida* Loew

In Europe the following species seem to have this seasonal distribution:

*Tipula cava* Ried.
*livida* v. d. W.
*Tipula trifasciata* Loew
*vernalis* Meig.

Midsummer to late summer species — from August 10 to September 10 — are as follows:

*Dicranomyia longipennis* (Schum.)
*Limnobia solitaria* O. S.
*Erioptera parva* O. S.
*Adelphomyia americana* Alex.
*cayuga* Alex.
*Tricyphona autumnalis* Alex.
*katahdin* Alex.
*Tipula abdominalis* (Say)
*sayi* Alex.
*unimaculata* (Loew)

In Europe the following species seem to have this seasonal distribution.

*Tipula bifasciculata* Loew
*dilatata* Schum.
*Tipula fulvipennis* DeG.
*helvola* Loew

Autumnal species — from September 10 to snowfall — are as follows. *Limnophila ultima* is sometimes vernal but is commoner in late summer and autumn. *Discobola argus* is found at other seasons but is more numerous in September. *Cladura flavoferruginea*, *Limnophila ultima*, and *Tipula cunctans* have a longer flight-period than most of the others listed.

*Dicranomyia brevivena* O. S.
*Limnobia parietina* O. S.
*Discobola argus* (Say)
*Cladura delicatula* Alex.
*flavoferruginea* O. S.
*Limnophila osborni* Alex.
*ultima* O. S.
*Tricyphona autumnalis* Alex.
*Tipula cunctans* Say
*fragilis* Loew
*ultima* Alex.
*unifasciata* (Loew)

The following European species seem to have this seasonal distribution:

*Tipula anonyma* Bergr.
*autumnalis* Loew
*interserta* Ried.
*luteipennis* Meig.
*marmorata* Meig.
*Tipula melanoceros* Schum.
*obsoleta* Meig.
*pagana* Meig.
*rufina* Meig.
*signata* Staeg.

## IMMATURE STAGES

### THE EGG

The egg stage is generally of short duration, usually lasting from one to three weeks. In *Tipula sayi* it is eight days. The number of eggs laid, so far as is known, ranges from about forty-five in *Styringomyia didyma* to about two thousand in the larger species of Eriocera. The eggs are deposited in different ways according to the species, the details of which are discussed elsewhere (page 881).

The eggs are without an intricate sculpturing, but may be finely punctured or striate. They are black, with a heavy chorion in the Tipulinae and in the tribe Hexatomini. In most of the Limnobiinae and the Cylindrotominae they are white and pellucid, or even a light orange-red in some cases, as in the genus Dicranomyia.

### THE LARVA

The larval, or feeding, stage is the longest in the life of a crane-fly, in the known cases requiring the greater part of the year. Some of the smaller forms are presumably double-brooded, since they appear in the spring, are absent during most of the summer, and reappear in the late

summer and early fall. In such cases the larval existence is, of course, greatly shortened. The larval habitat is exceedingly varied and may be summarized as follows:[9]

*Tanyderidae.*— Nothing whatever is known of the immature stages of this group of flies, and it is very desirable that some of the forms should be reared. They are very rare, however, and even the adults are uncommon in collections. It is very probable that the larvae of species of Protoplasa, the only genus in the Northern Hemisphere, will be found to be amphibious, such a larval habitat often characterizing primitive forms.

*Ptychopteridae.*— Semi-aquatic or amphibious (Ptychoptera, Bittacomorpha, Bittacomorphella).

*Rhyphidae.*—In decaying vegetable and animal matter (Trichocera, Mycetobia, Rhyphus).

*Tipulidae.*— Limnobiini: Aquatic, in silken cases or tubes among submerged mosses (*Dicranomyia simulans*); semi-aquatic or in moist earth (*Limnobia fallax*, and probably *L. solitaria* and *L. parietina*); in decaying vegetable matter (*Limnobia indigena, Rhipidia domestica*); in decaying wood and under the bark (*Dicranomyia rara, D. macateei, D. dumetorum*, Discobola, *Limnobia cinctipes, L. annulus, Rhipidia bryanti, R. fidelis*, and others); in fungi (*Limnobia xanthoptera, L. triocellata*, and sometimes *L. cinctipes*). The Hawaiian species *Dicranomyia foliocuniculator* Swezey mines in the leaves of gesneriaceous plants (Cyrtandra), forming long, tortuous tunnels.

Antochini: Aquatic, very similar to habitat of *Dicranomyia simulans* as described above, in silken cases on rocks that are thoroly wet (Elliptera); in submerged stems of *Rumex aquaticus* (*Rhamphidia longirostris*); in slow or rapid water on stones (Antocha); in moist earth or mud (*Toxorhina muliebris*); under the bark of decaying trees (*Elephantomyia westwoodi, Teucholabis complexa*).

Eriopterini: In moist earth or mud in close proximity to water (most species of the tribe — *Ormosia nubila, O. innocens, O. meigenii, O. nigripila, Erioptera chlorophylla, E. vespertina, E. septemtrionis, Molophilus pubipennis, Helobia hybrida, Gonomyia sulphurella*, and others); in earth of a somewhat drier nature (Chionea); in wet sandy soil (*Gonomyia alexanderi*); under the bark of decaying trees (*Gnophomyia tristissima*). The tropical species of Trentepohlia live in decaying vegetable matter, or, as in the case of the two American species *T. bromeliadicola* and *T. leucoxena*, in the water gathered in the axils of bromeliaceous plants.

Limnophilini: Aquatic (*Limnophila luteipennis* and others); in wet or saturated organic mud in close proximity to running or standing water (most species of the tribe — *Limnophila macrocera, L. tenuicornis, L. tenuipes, L. recondita, L. adusta*, Adelphomyia, and others); in decaying wood and under the bark (*Epiphragma fascipennis, E. solatrix, E. picta, Limnophila unica*, and others); in fungi (*Ula elegans, U. macroptera*, and others).

Hexatomini: Aquatic in the early larval stages, going to land only when fully grown and ready to transform to the pupal condition; in sandy soil in close proximity to rather large streams or rivers (*Eriocera spinosa, E. longicornis, E. fultonensis, E. tristis, Hexatoma megacera*, and others); in organic earth and rich humus (*Penthoptera albitarsis*). As stated elsewhere, the larvae of this tribe are carnivorous, the larger species feeding on organisms as large as the nymphs of dragon-flies.

Pediciini: Aquatic or amphibious (probably all the species of the tribe — *Pedicia albivitta, P. rivosa*, Tricyphona, *Rhaphidolabis tenuipes, R. flaveola, Dicranota bimaculata*, and others). As stated elsewhere, the larvae of this tribe are carnivorous, those of the species of Dicranota feeding on worms of the genus Tubifex.

Cylindrotominae: Aquatic, on submerged plants and similar places (*Phalacrocera replicata*); in mountain torrents on the aquatic moss Fontinalis (*Triogma trisulcata*). Terrestrial, on leaves of flowering plants, as species of Anemone, Stellaria, Viola, and other genera (*Cylindrotoma distinctissima*); on mosses of the genus Hypnum and related species (*Liogma*

[9] The following entomologists have kindly supplied the writer with specimens or data on certain species as follows: Johannsen, *Limnobia fallax*; Greene, *L. indigena*; Shannon and Knab, *Rhipidia bryanti*; Mrs. Tothill, Toxorhina; Johnson and Shannon, Elephantomyia; Hyslop, Oropeza and Longurio.

*glabrata*, *L. nodicornis*). The larvae of this group are usually bright green in color, are variously armed with spines and filaments, and bear a striking resemblance to the caterpillars of certain Lepidoptera.

Dolichopezini: In decaying wood (*Brachypremna dispellens*); underneath the moss *Hedwigia albicans*, but also in moist earth (Oropeza).

Ctenophorini: In decaying wood (*Ctenophora apicata* and others); in wood that is but slightly decayed (Tanyptera). The species of the latter genus bore into the wood of Acer and other hardwood trees while it is still in a good state of preservation, and represent the maximum development of the wood-boring habit in this family so far as is known to the writer.

Tipulini: Aquatic, but going to the land for pupation (*Tipula abdominalis*, *T. cayuga*, *T. tephrocephala*, and others); semi-aquatic or amphibious (*Holorusia rubiginosa*, Longurio, *Tipula bella*, *T. sayi*, *T. strepens*, *T. tricolor*, and others); under moss growing on moist earth (*Tipula nobilis*, *T. collaris*, and others); in drier soil feeding on the tissue of plants (*Tipula ultima*, *T. bicornis*, *T. cunctans*, *Nephrotoma ferruginea*, and others); under bark of prostrate trees in an advanced state of decay (*Tipula usitata*, *T. trivittata*, and others). The green larvae of an undetermined Tipula (possibily *T. iroquois*) live in submerged mosses (Hypnum, sens. lat.) in rapid-flowing streams where the current is very strong; here they are associated with a society which is characteristic of such places — may-flies (*Iron fragilis*), black-flies (Simulium), net-winged midges (Blepharocera), Stratiomyiidae, Anthomyiidae, *Limnophora torreyae*, and a host of other forms.

The larva of the crane-fly has a segmented body, with about twelve apparent segments; the head is a composite of several small sclerites. The larva is wormlike in appearance and is legless, and the head is capable of retraction within the body except in the Ptychopteridae and the Rhyphidae. At the caudal end of the body is the disk bearing the two spiracles, or stigmata. Except in the Limnobiini this disk is surrounded by a varying number of fleshy lobes — two in the Pediciini (fig. 122, E), four in many of the Tipulinae, the Cylindrotominae (fig. 122, G), the Antochini, and the Hexatomini (fig. 122, F), five in the Eriopterini, the Limnophilini (fig. 122, D), and many of the Tipulinae, and six or eight in other species. Beneath the spiracular disk are the gills, usually four or six in number. These are long and filiform in the aquatic species (fig. 122, I), and correspondingly reduced or entirely absent in the less aquatic and the terrestrial species. In the Ptychopteridae (fig. 122, A) the spiracles are borne at the tip of a long, extensile tube, which is raised above the surface film while the larva feeds at will beneath the water; the gills, two in number, are about midlength of the tube. The larva of Trichocera has a pair of thoracic stigmata in addition to the caudal spiracles.

In many crane-fly larvae the body is provided with fleshy transverse folds, which are armed with chitinized points and roughened areas to assist in locomotion. These are best developed in the Pediciini (fig. 122, E), in which they resemble pseudopodia. The larvae of the Cylindrotominae (fig. 122, H) are covered with spines and thorns of various shapes.

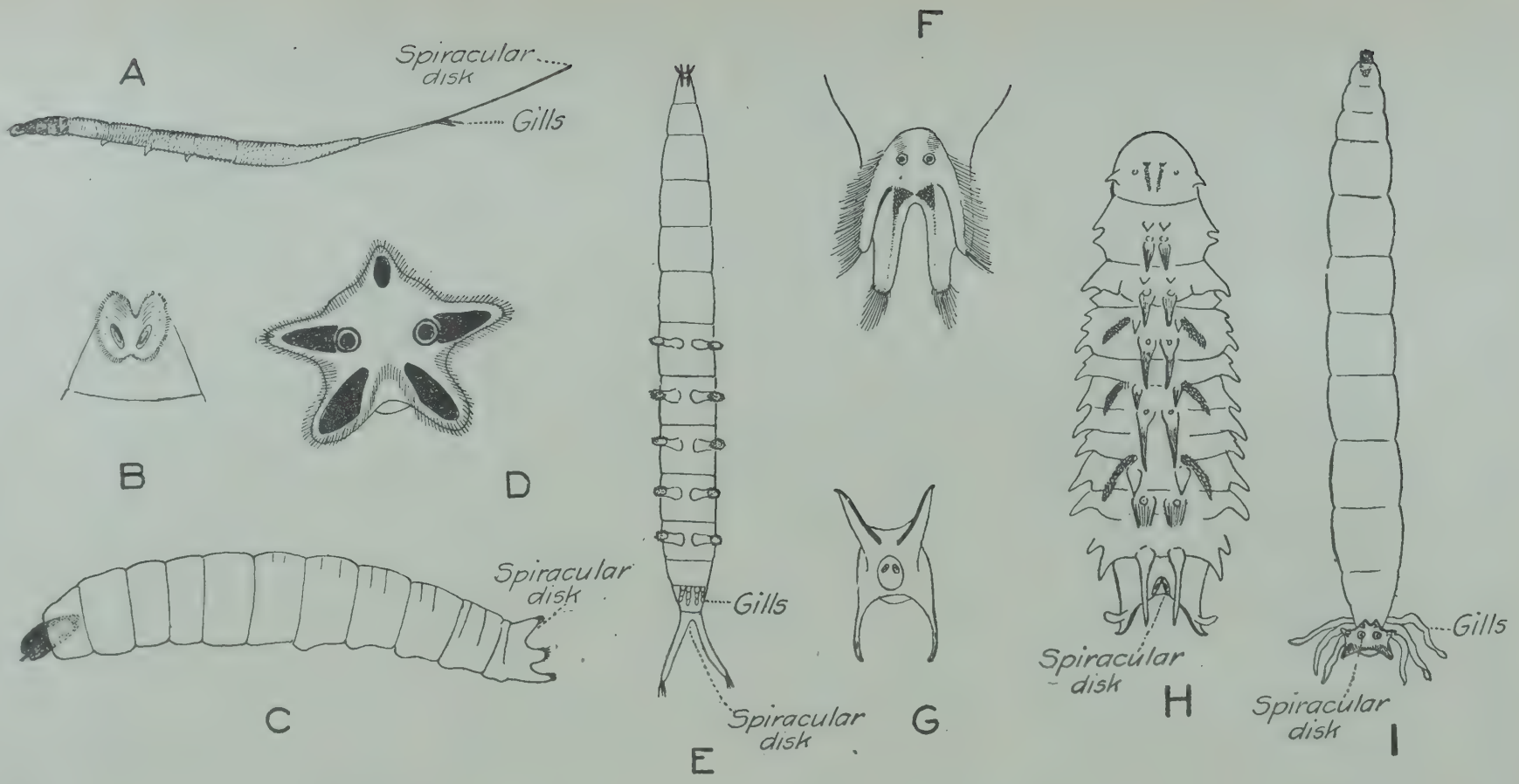


FIG. 122. LARVAE OF VARIOUS SPECIES OF CRANE-FLIES

A, *Bittacomorpha clavipes* (Ptychopteridae), lateral aspect; after Hart. B, *Dicranomyia simulans* (Limnobiini), spiracular disk; after Needham. C and D, *Ula elegans* (Limnophilini), lateral aspect and spiracular disk. E, *Dicranota bimaculata* (Pediciini), ventral aspect; after Miall. F, *Hexatoma megacera* (Hexatomini), spiracular disk. G and H, *Liogma nodicornis* (Cylindrotominae), spiracular disk and dorsal aspect. I, *Tipula* sp., *tricolor* group (Tipulini), dorsal aspect

### THE PUPA

The pupal stage is of short duration, usually a week or two, and is spent in or near the larval habitat. In the case of aquatic species the pupal existence is passed in the earth adjoining the water in which the larva lived, except perhaps in the case of Antocha, which may pupate directly in the water. The larvae of many species of Limnobiini, of Antochini, and in a slightly lesser degree of most other groups, spin a silken case, or cocoon, in which to spend the pupal period. The pupae are more or less active and often wriggle about with great agility.

On the thoracic dorsum the pupa bears the two breathing horns (fig. 123), which are variously formed in the different groups. They are short, blunt, and flattened in the Limnobiini (fig. 123, B), moderately elongate and cylindrical in the Eriopterini, the Limnophilini (fig. 123, C and D), and the Tipulini (fig. 123, H), short and truncated at their apices in the Pediciini (fig. 123, E). In the Ptychopteridae (fig. 123, A), one of the two horns is atrophied, while the other is enormously elongated and serves the same function as the extensile breathing tube of the larva. In addition to the thoracic spiracles, the pupae of the Hexatomini (fig. 123, F), the Eriopterini, and some others have conspicuous lateral abdominal stigmata.

The abdominal segments generally have rows of spines or chitinized points arranged transversely around the caudal margin (fig. 123, H), which help the insect in moving about and serve to keep the tender part of the abdomen from contact with the earth. In the Hexatomini (fig. 123, F) similar spines are developed on the thorax, on the head, and even on the face of the compound eye. In the Cylindrotominae (fig. 123, G) these spines are very highly developed. Smooth-bodied pupae, such as are found in the Limnobiini, are usually inclosed in a silken tube which keeps them from contact with the soil.

When the insect is ready to transform to the final, or adult, stage, the pupa makes its way to the surface of the earth, to which it remains attached by the caudal part of the abdomen. The thoracic notum then splits down the mid-dorsal region in a straight line, and thru this opening the adult fly emerges. Before the chitin of the body hardens, the insect is very weak and pallid, but in a short time the body expands to its full size and becomes hardened and fully colored, and the dangerous period of transformation is over.

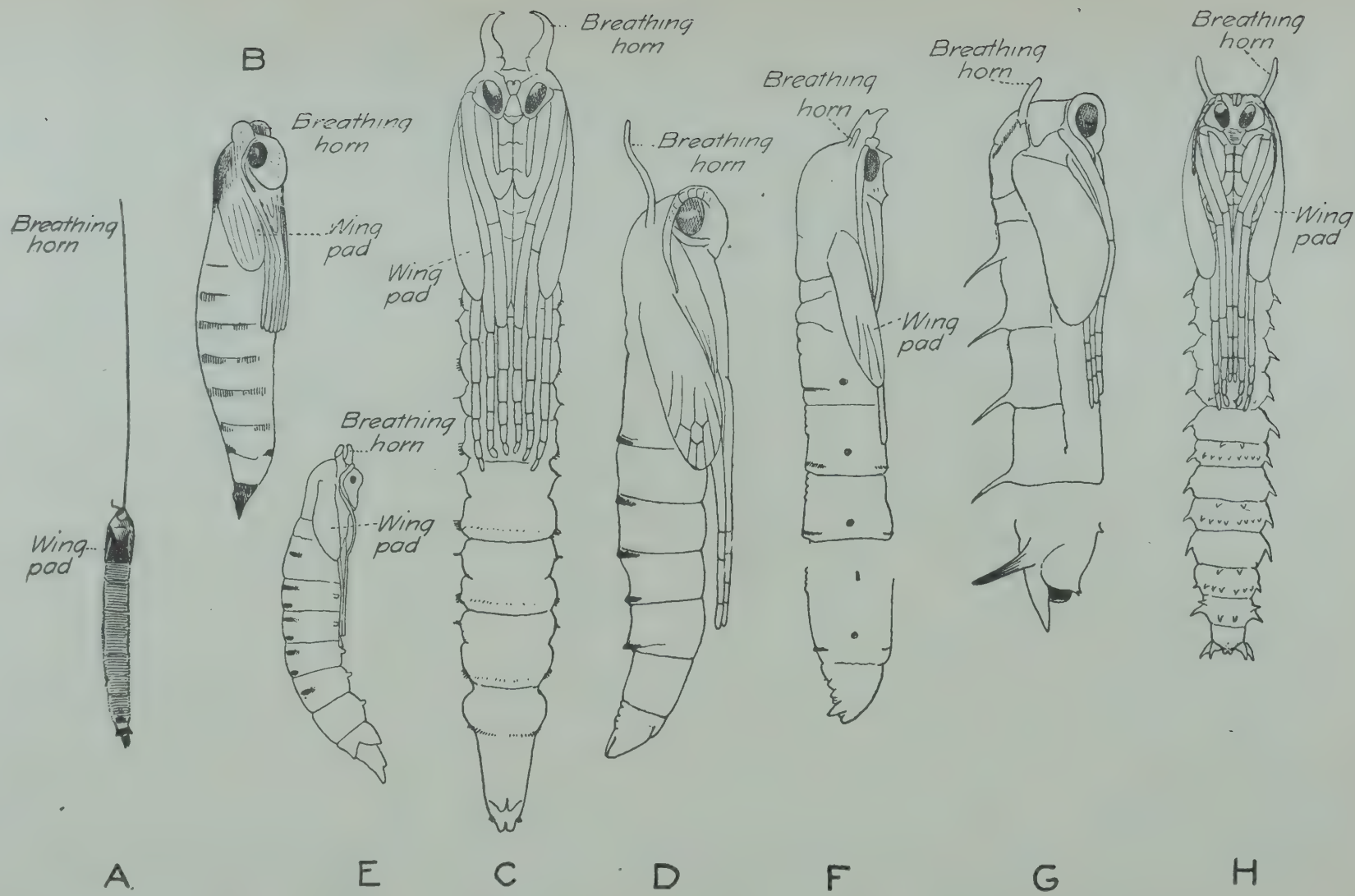


FIG. 123. PUPAE OF VARIOUS SPECIES OF CRANE-FLIES

A, *Bittacomorpha clavipes* (Ptychopteridae), dorsal aspect; after Hart. B, *Limnobia cinctipes* (Limnobiini), lateral aspect. C, *Epiphragma fascipennis* (Limnophilini), ventral aspect; after Needham. D, *Ula elegans* (Limnophilini), lateral aspect. E, *Dicranota bimaculata* (Pediciini), lateral aspect; after Miall. F, *Hexatoma megacera* (Hexatomini), lateral aspect. G, *Liogma nodicornis* (Cylindrotominae), lateral aspect. H, *Tipula ultima* (Tipulini), ventral aspect; after Needham.

### REARING THE IMMATURE STAGES

As has been stated elsewhere, the author believes the most important work yet to be done in entomology is the study of the immature stages of the various groups of insects. In most cases it is necessary to rear the immature stages thru to the adult in order to be certain of the species, and this process of bringing the larva to the perfect condition is often attended with many difficulties. The author has spent several years in rearing the local Tipulidae, and a general statement of the methods adopted is here given.

It should be borne in mind that the bringing of the larvae from their natural habitat into the warmth of the laboratory accelerates their development, and the adults emerge in the breeding cages a week or two earlier than in nature.

#### *Aquatic forms*

The aquatic forms are among the most difficult to rear, especially the species living in rapid, well-aërated water. It must be understood at the start that practically all crane-flies require earth, sand, or a similar solid material in which to pupate, and it is often very difficult to provide rushing torrents for the larval life together with solid earth for the pupal existence. Breeding cages, consisting of wire cylinders the ends of which are covered with cheesecloth, have been used with considerable success. The mesh must be of sufficient fineness to retain the larvae inside, but not so small as to exclude the food that is carried in the current; however, since this food is microscopic or very small, a fine mesh is sufficient to allow its entry into the cage. The whole cage can be transferred to the natural haunt of the larva and kept under observation until the adult insect emerges. The main difficulties with this method are the danger of smothering the insect by deposition of silt during high water, the washing away of the entire outfit during storms, and the inconvenience, in most cases, of having to make many long trips to the scene of rearing before the final result is obtained. In almost all cases when the species could be reared by the use of such breeding cages, the writer has been able to get adult flies by placing the full-grown larvae in medium-sized (four-ounce) shell vials together with some earth from their natural habitat. In order to prevent evaporation, small caps of cheesecloth may be fas-

tened over the ends of the vials by means of rubber bands, sufficient water being added every day or two to restore the balance lost by evaporation. If the specimens are fully grown or nearly so, they soon pupate and finally emerge.

Species that live in extremely rapid waters (as the tipuline larva described on page 839) are almost impossible to rear. The best results have been obtained by placing the fully grown larvae in the folds of a saturated piece of cheesecloth in a jar, the jar being corked to prevent any evaporation — which is here, as elsewhere, the most frequent source of danger and death to the larvae. Several specimens of crane-fly larvae may be placed in a single vial except in the case of the carnivorous forms (Hexatomini, Pediciini), in which case care should be taken to isolate single specimens lest they kill one another and the decaying of their bodies destroy the remaining life in the vials.

*Mud-inhabiting forms*

The majority of crane-fly larvae are mud-inhabiting forms. Most of these belong to the small and inconspicuous Limnobiinae, and are rarely seen by the collector. To procure them it is necessary to sift the mud of their haunts and examine the contents of the sieve with great care. A small-mesh wire sieve is about the most satisfactory form to use, and the mud can be washed in small quantities and the remaining contents of the sieve easily scrutinized. As they are found, the larvae can be placed in water in small watch crystals and finally removed to individual breeding jars. The methods of breeding described above are applicable to these, and if the larvae are large and nearly grown it is not difficult to rear them.

*Fungus-inhabiting forms*

The forms inhabiting fungi (species of Limnobia and Ula, and some others) are easily reared by placing the whole fungus in a large pint or quart jar about one-fourth filled with pure sand. This sand takes up the juices as the fungus decays, and at the same time furnishes a good place for pupation of the species. The jars should be kept air-tight to retain a balance in moisture conditions.

*Wood- and bark-inhabiting forms*

The forms inhabiting wood and bark (Ctenophora, Tanyptera, and others) may be reared by placing pieces of their natural habitations in a large closed jar and leaving them undisturbed. Pupation takes place in the burrows of the larvae.

## THE ADULT FLIES

### STRUCTURE

#### *The head*

The head is the first, or anterior, region of the body. It bears the mouth parts, the antennae, the compound eyes, and, when they are present, the simple eyes, or ocelli.

*The sclerites*

The sclerites, or segments, composing the head are approximately the same as in other insects, consisting of a prominent dorsal sclerite which surrounds the compound eyes, the *epicranium*. This is further divided into regions which may be located generally as follows: The *fronto-clypeus* is located on the dorso-cephalic aspect of the head, between the labrum and the region of the vertex. It consists of the united front and clypeus, the suture between them having disappeared. The *labrum*, or upper lip, is often present as a chitinized linear structure lying anterior to the fronto-clypeus and attached to the ventral margin of the clypeal region of the latter. The *vertex* occupies the dorsal region between the compound eyes, and, when they are present, includes the ocelli, or simple eyes. On or near its anterior part it bears the antennae (page 848), inserted in depressions, the *antennal fossae*. In many species with elongate antennae, especially in Eriocera, Macromastix, and some other genera, the vertex bears a distinct tubercle, the *vertical tubercle*, which is often deeply bifid. In *Geranomyia cornigera* Alex. (Philippine Islands) the vertex bears a curious elongate fleshy lobe. Very rarely this sclerite bears three simple eyes, or ocelli, which are discussed elsewhere (page 854). The *genae*, or cheeks, occupy the sides, or lateral parts, of the head, ventrad and mesad of the compound eyes. The ventro-caudal region of the head is made up of the *postgenae*. The dorso-caudal region is the *occiput*.

*The mouth parts*

In many species in widely separated tribes, the anterior, or frontal, part of the head is produced into a short, cylindrical rostrum, which is in most cases nearly if not quite as long as the head itself. Such a frontal prolongation occurs in Rhamphidia (fig. 124, B and C), in some tropical species of Teucholabis (Antochini), in Opifex (Eriopterini) and Ornithodes (Pediciini), and in most Tipulini (fig. 124, E). In these

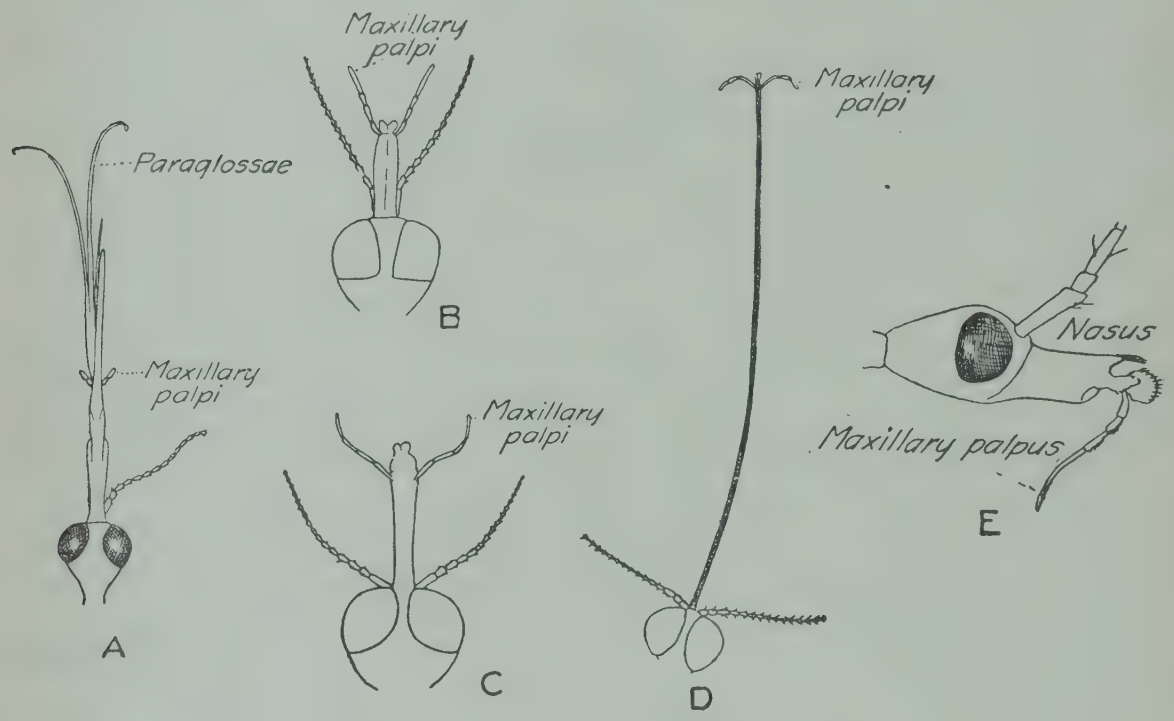


FIG. 124. MOUTH PARTS OF VARIOUS SPECIES OF CRANE-FLIES

A, *Geranomyia canadensis*, male, ventral aspect. B, *Rhamphidia flavipes*, male, ventral aspect. C, *Rhamphidia mainensis*, male, ventral aspect. D, *Elephantomyia westwoodi*, male, ventral aspect. E, *Tipula apicalis*, male, lateral aspect

cases the mouth parts are borne at or near the tip of the prolongation. In the Tipulini there often appears near the end of the prolongation, on the dorsal side, a small tubercle bearing a brush of long hairs (fig. 124, E). This is the *nasus*, or "nose." The most generalized condition of the mouth parts in this group of flies is seen in certain members of the primitive group Tanyderidae, in which the labrum, the maxillae, the labium, and possibly the mandibles, are distinct and styliform (Alexander, 1913a:332–333).

The mouth parts and the head capsule of the Diptera have been studied recently by Peterson (1916). The following summary of the mouth parts is taken largely from his paper:

The *maxillae* are the paired organs lying below the labrum and above the labium, one on either side. In generalized forms, such as Trichocera, they consist of a small triangular *cardo*, an elongate *stipes* bearing the needle-like *galea*, and the *palpus*. The maxillary palpi are primitively five-segmented but in almost all crane-flies only four segments are apparent; in certain cases the reduction in segments is rather extreme; this is discussed more in detail below. In the Limnobiini (Limnobia, Geranomyia) the stipites are entad of the postgenae and have their proximal ends united. In the Tipulini (Tipula) the two stipites are completely united along their inner margin to form a single median plate. The galeae are prominent in Trichocera, but are very reduced in Geranomyia and are entirely lacking in Tipula.

The *labium*, or lower lip, is the ventral, or posterior, unpaired organ. It consists of a basal immovable part, made up of the *mentum* and the *submentum*, and a movable part, or *ligula*, the basal sclerites of which are called by Peterson the *thecae*, the *furcae*, and so on, and the distal parts the *glossae* and the *paraglossae*.

The *epipharynx* lies behind the labrum and fuses with it to form the *labrum-epipharynx*. The *hypopharynx* is the prolonged cuticular lining of the opposite side of the mouth cavity. In such genera as Trichocera, Limnobia, and Tipula, studied by Peterson, the labrum-epipharynx and the hypopharynx are short, but in Geranomyia, which has an elongate rostrum, these parts are correspondingly elongated.

There are two tribes containing one or more genera in which the mouth parts are greatly elongated, being in many instances longer than the remainder of the body. In the tribe Limnobiini the genus Geranomyia is thus characterized, and in the tribe Antochini the genera Elephantomyia, Rhampholimnobia, Ceratocheilus, and Toxorhina. These may be discussed briefly.

In Geranomyia (fig. 124, A) the most evident parts of the beak are styliform and greatly elongated, consisting of the labrum-epipharynx, the hypopharynx, and the conspicuous divergent lips, the paraglossae, which extend far beyond the other elements; the maxillary palpi are located far back on the organ at about one-third its length, and are reduced in

number of segments from four in the generalized subgenus Tetraphana to one in the subgenus Monophana. In Elephantomyia (fig. 124, D), Rhampholimnobia, Ceratocheilus, and Toxorhina, the rostrum consists of a much elongated tube which bears the reduced mouth parts and the maxillary palpi at the extreme apex; in Elephantomyia the maxillary palpi are three-segmented, while in Toxorhina they are apparently single-segmented.

Those species of Geranomyia, Elephantomyia, and Toxorhina whose feeding habits are known, all feed on the nectar of tubular flowers, such as the Compositae, the Apocynaceae, the Ericaceae, the Umbelliferae, the Rhamnaceae, and the Lauraceae.

The maxillary palpi are generally four-segmented; in the primitive group Tanyderidae they are five-segmented. By reduction there are found one, two (fig. 124, A), three, or four segments, respectively, in the four subgenera of Geranomyia; there are three in Elephantomyia (fig. 124, D), and apparently only one in Toxorhina. The segments in most Limnobiinae are approximately subequal in size, but in the genus Pedicia and in the subfamily Tipulinae (fig. 124, E) the fourth segment is greatly elongated, whiplash-like, and usually longer than the three preceding segments taken together. The labial palpi are two-segmented and conspicuous in species of Trentepohlia.

*The antennae*

The antennae of crane-flies present many interesting conditions, both in the number of the segments of which they are composed and in their structure, and many generic names have been based on these conditions — Trichocera, Rhipidia, Trimicra, Rhabdomastix, Sigmatomera, Ctenodonia, Polymera, Hexatoma, Eriocera, Cylindrotoma, Phalacrocera, Megistocera, Ctenophora, and others.

The antennae are inserted on the vertex between the compound eyes. The diversity in their structure is considerable, and consists of great elongation of the organ, constriction of the segments, and the appearance of pectinations and flabellate formations. These are sexual characters only and are confined to the male sex. Elongation of the antennae occurs in many widely-separated tribes; moderate elongation is found in a wide range of native Ptychopteridae, in Trichocera, and in the tipuline genera Atarba, Ormosia, Molophilus, Limnophila, Penthoptera, Dicranota,

Nephrotoma, and Tipula; great elongation, in which the organ may be two or more times as long as the whole body, is found in a few native species of Eriocera (fig. 125, F), and in some exotic genera, as Rhabdomastix, *sens. str.*, the Old World species of Megistocera, and a few species of Macromastix. The flagellar segments are constricted at their middle in the genus Polymera, producing the multi-segmented appearance which gives the genus its name; in Sigmatomera some of the flagellar segments are reniform or shaped like a recumbent S. In many species of Ormosia (*O. monticola*, *O. divergens*, *O. megacera*, *O. mesocera*) the elongated antennae are subnodulose and strongly suggest the beadlike condition obtaining in the Cecidomyiidae. In Trimicra the three terminal segments are abruptly smaller than the remainder of the flagellum; in some species of Stygeropis it is the terminal segment only that is so reduced. Pectinations and flabellate formations are found in the antennae in many genera — Rhipidia (fig. 125, A and B), Gynoplistia, Cerozodia, Ctenonia, most of the genera of the tribe Ctenophorini (fig. 125, L and M), and several genera of the tribe Tipulini, such as Ptilogyna and Ozodicera.

The two basal segments of the antennae are quite different in shape from those that follow, and are called the *scapus*, or *scape*. The scape is often considerably enlarged, especially in those species with elongate antennae — in the genera Rhabdomastix, Eriocera (fig. 125, F), Megistocera, and others. The second segment of the scape is usually shorter than the first, and in the species with elongate antennae it is usually short and cup-shaped (fig. 125, F, G, and H), a condition known as cyathiform. The whiplike part beyond the scape is the *flagellum*. The flagellum is almost always clothed with a pubescence of varying character, from straight to uncinate, from appressed to outspreading and divergent, from short to long, and often longer in the male sex than in the female. In addition to these delicate hairs there are usually strong, bristle-like hairs arranged in a more or less complete whorl, or verticil (fig. 125, J and O). The Tipulinae (fig. 125, L–O) have a more or less complete whorl of these strong hairs, which are absent in Stygeropis (fig. 125, N) and in Holorusia and form good generic characters in a difficult group of the family. In many species of Gonomyia (*G. sulphurella* [fig. 125, E], *G. manca*, *G. pleuralis*, *G. amazona*, and others), and in some species of Erioptera (subgenus Empeda), the verticillate hairs on the male antennae are exceedingly elongated and conspicuous.

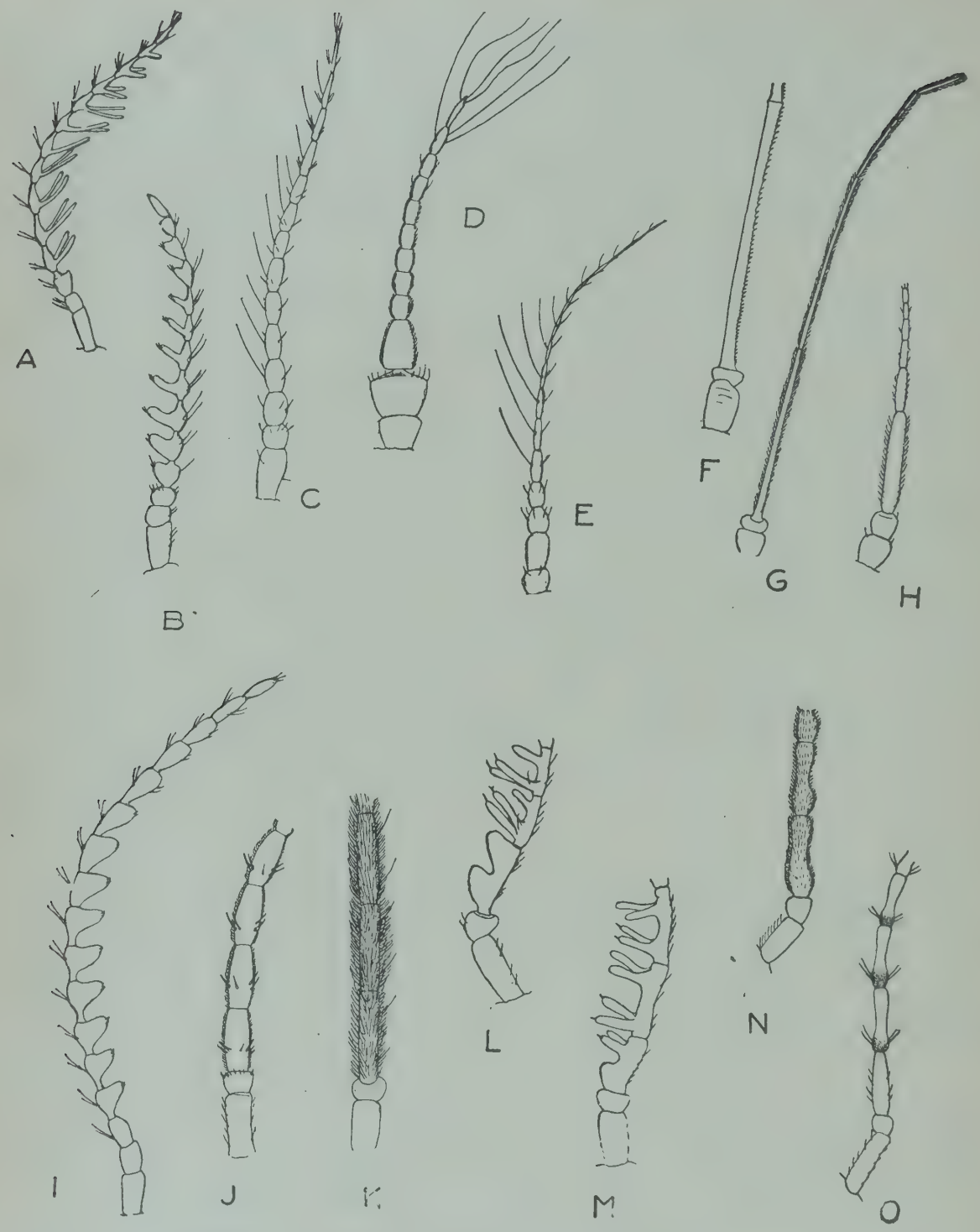


FIG. 125. ANTENNAE OF VARIOUS SPECIES OF CRANE-FLIES

Limnobiinae: A, *Rhipidia maculata*, male; B, *Rhipidia fidelis*, male; C, *Limnobia tristigma*, male; D, *Toxorhina brasiliensis*, male; E, *Gonomyia sulphurella*, male; F, *Eriocera spinosa*, male, three basal segments; G, *Hexatoma megacera*, male; H, *Hexatoma megacera*, female

Cylindrotominae: I, *Liogma nodicornis*, male; J, *Phalacrocera tipulina*, male, six basal segments; K, *Cylindrotoma tarsalis*, male, five basal segments

Tipulinae: L, *Tanyptera frontalis*, male, five basal segments; M, *Ctenophora angustipennis*, male, five basal segments; N, *Stygeropis fuscipennis*, male, four basal segments; O, *Tipula mainensis*, male, six basal segments

The following additional notes on chiefly local species are presented:

*Tanyderidae*: In *Protoplasa fitchii*, of the family Tanyderidae, the antennae are 16-segmented; the scape is enlarged, and the flagellar segments are elongate-oval with a dense pubescence and verticillate bristles. In other Tanyderidae the number of segments ranges from 15 to 25.

*Ptychopteridae.*— In the genus Bittacomorpha of the family Ptychopteridae, the antennae are apparently 20-segmented. In the males they are elongated; the scape segments are short, the second one being short-cyathiform; the flagellar segments are greatly elongated, with a long outstretched pubescence and no bristles. In Ptychoptera the antennae are 16-segmented, with distinct scattered bristles and a short, somewhat uncinate, pubescence.

*Rhyphidae.*— In the genus Trichocera of the family Rhyphidae, the antennae are almost hairlike, tho finely pubescent.

*Tipulidae, Limnobiinae.*— Limnobiini: In the tribe Limnobiini the antennae are 14-segmented. In Limnobia (fig. 125, C) the segments have numerous bristles and a close, dense pubescence; the terminal segment is usually much attenuated, about as long as the two preceding segments taken together, often presenting a biarticulate appearance. In Rhipidia a curious modification of the organ is found, the flagellar segments being bipectinate in the subgenus Rhipidia (fig. 125, A), unipectinate in the subgenus Monorhipidia (fig. 125, B), and from subpectinate to almost normal in the subgenus Arhipidia.

Antochini: As a rule the antennae are 16-segmented in the tribe Antochini. The first scape segment is rather elongated, the second is oval, not markedly cyathiform. The flagellar segments are rounded-oval or elongate (in the males of most species of Atarba), with bristles and a short, dense pubescence. The antennae are of this normal structure in the genera Rhamphidia, Antocha, Dicranoptycha, Atarba, and Teucholabis. In Elephantomyia there are 15 segments; the first segment of the scape is only a little larger than the second; the first flagellar segment is apparently formed by the fusion of two segments, and bears three strong hairs on the lower face in a line; the remaining segments of the flagellum are elongate-cylindrical, with strong verticils. In the genera Toxorhina (fig. 125, D) and Ceratocheilus there are but 12 segments; the second scape segment is larger than the first; the first flagellar segment is obconical, and is apparently formed by the fusion of five segments,

altho the segment is very short and is destitute of verticils; the seven succeeding flagellar segments are short-cylindrical, without verticils; the terminal two segments are more elongated and each bears about three very long hairs.

Eriopterini: Normally there are 16 antennal segments in the tribe Eriopterini. In some genera both elongate and short antennae are found in the same group, as in Ormosia, *sens. str.* In Chionea, Cladura, Pterochionea, and Crypteria the number of antennal segments is reduced, due to the fusion of several segments to make up the basal segment of the flagellum — as in the case of Toxorhina, already discussed — this fusion segment including usually five segments.

Limnophilini: In the tribe Limnophilini the antennae are normally 16-segmented; in the genus Ula they are 17-segmented. In Limnophila and Epiphragma are found some species with elongate and others with short antennae. In *Limnophila macrocera* and some other species, the segments of the flagellum are provided with abundant outstretched hairs. In *Adelphomyia cayuga* the basal segments of the flagellum are fused into an indistinct fusion-segment; the other local species of this genus have normal antennae.

Hexatomini: In *Hexatoma megacera* (fig. 125, G) the antennae of the male are 6-segmented, the flagellar segments being elongate; in the female (fig. 125, H) the antennae are apparently 8-segmented. In Eriocera there are many species with short antennae (*Eriocera brachycera*, *E. fuliginosa*, *E. fultonensis*, and others), species with the antennae intermediate in length (such as *E. eriophora*), and numerous species with greatly elongated antennae (*E. spinosa*, *E. californica*, *E. longicornis*, and others). In *E. spinosa* (fig. 125, F), *E. longicornis*, and others, the lower surface of the basal flagellar segment is provided with numerous spines, regularly spaced, pointing toward the tip of the organ; the manner in which these spines are used in extricating the organ from the antennal sheath of the pupa is described by Alexander and Lloyd (1914). In *E. wilsonii* the antennae are likewise elongated in the male sex, but are provided with a strong pubescence, the spines being quite lacking. Most species of Eriocera have short antennae in both sexes.

Pediciini: In the genera Pedicia and Tricyphona of the tribe Pediciini, the antennae are 16-segmented; in the genus Dicranota and the subgenera

Plectromyia and Rhaphidolabis, they are 13-segmented; and in the subgenus Rhaphidolabina they are 15-segmented.

*Tipulidae, Cylindrotominae.*— The antennae are apparently 16-segmented in the genus Cylindrotoma of the subfamily Cylindrotominae, and 17-segmented in the genera Phalacrocera and Liogma. In *Cylindrotoma tarsalis* (fig. 125, K) the flagellar segments in the male are elongate-cylindrical, with a dense erect pubescence and a very few scattered bristles. In *Phalacrocera tipulina* (fig. 125, J) the condition is fairly similar, but there is a distinct verticil of stiff bristles near the bases of the segments, a condition strongly suggesting that found in the genus Tipula. In *Liogma nodicornis* (fig. 125, I) the intermediate flagellar segments are rather strongly pectinate, with a dense, pale pubescence and several long bristles on the back face of each segment, and with shorter, weaker bristles at the apex of the pectination.

*Tipulidae, Tipulinae.*— Dolichopezini: The antennae in Dolichopeza, Oropeza, Brachypremna, and other genera of the tribe Dolichopezini, are normally 13-segmented; in the American species of the genus Megistocera the antennae are 8-segmented. The organ is often considerably elongated, exceedingly so in Old World species of Megistocera. In Brachypremna the antennae are correspondingly short and tiny.

Ctenophorini: In the tribe Ctenophorini the antennae are 13-segmented. In the male sex they are curiously pectinated or fanlike, tho differing in construction from those in Rhipidia already discussed (page 851). In *Ctenophora angustipennis* (fig. 125, M) the first segment of the flagellum bears a basal pectination and two apical pectinations, each tipped with a bristle; the second and succeeding segments have a basal pair of pectinations, each tipped with a bristle, and a pair of apical appendages, untipped. In *Tanyptera frontalis* (fig. 125, L) the first segment of the flagellum bears a basal and an apical pectination; the second and succeeding segments have a basal pair of pectinations, each tipped with a bristle, and the single shorter apical pectination is not thus protected.

Tipulini: Normally the antennae in the tribe Tipulini are 13-segmented; in some species of Nephrotoma there are 16 or 19 segments in the male. In most species of this tribe each flagellar segment has a strong basal swelling armed with a verticil of strong bristles; this knobbed condition reaches its maximum development in the species of the *monilifera* group (of tropical America), in which a beadlike form is produced. Other

species of Tipula and some species of Nephrotoma have the segments deeply incised on the under face, producing a serrated appearance. In Stygeropis (fig. 125, N) and Holorusia, and to a lesser extent in Longurio, the verticils are lacking. *Tipula mainensis* (fig. 125, O) is a typical Tipula and illustrates this verticillate condition.

*The eyes*

On either side of the head, in all crane-flies, are the large compound eyes, made up of numerous facets, or *ommatidia*. In generalized forms the facets are large and coarse, so that the eye presents a coarsely granulated appearance; in other species the ommatidia are so small and abundant that the surface of the eye appears very smooth and regular. In most species of Tipulidae the eyes are separated by a narrow strip of the front (*dichoptic*), but in the males of some they are contiguous (*holoptic*) or nearly so, as in certain species of Rhipidia and allied groups. In some species of Erioptera (*Erioptera macrophthalma, E. vespertina, E. nyctops,* and others) the eyes of the males are much larger than those of the females and are contiguous beneath.

In most genera the eyes are large and extend backward onto the caudal part of the head. In Trichocera and Ischnothrix the vertex bears three simple eyes, or *ocelli*.

*The thorax*

The thorax is the second region of the body and lies between the head and the abdomen. This part of the body bears the legs, and, when they are present, the wings also. It is divisible into three subregions, as follows: the prothorax, or first segment, which bears the fore legs; the mesothorax, or second segment, which bears the middle legs and the wings; and the metathorax, or third segment, which bears the hind legs and the halteres. The upper, or dorsal, sclerites of these subregions are called the *tergites*, the *notum*, or the *dorsum*; the lateral sclerites, those on the sides of the body, are the *pleura*, or *pleurites*; those on the lower, or ventral, parts of the body are the *sternites*, or *sternum*. Each subregion has its own terminology, the prothorax having its pronotum, propleurites, and prosternum, the mesothorax its mesonotum, mesopleurites, and mesosternum, and so on. The legs borne by these respective segments likewise have the corresponding prefix applied to their parts — as the precoxa (or fore coxa), the mesocoxa (or middle coxa), the pre-

femora, the mesotibia, and so on. In addition to the thoracic segments there are some tiny sclerites between the head and the prothorax, called the *cervical sclerites* and comprising the *neck*, or *microthorax*.

*The prothorax.*— In the Tipulidae the pronotum, or dorsal sclerite of the prothorax, consists of two regions which are usually interpreted as being homologous to the scutum and the scutellum of the mesonotum, described and illustrated below. In this paper these regions are called the *pronotal scutum* and the *pronotal scutellum*. The propleurites are made up of the usual pleural plates, which are discussed in the description of the mesothorax; these are termed the *proepisternum* and the *proepimeron*. The sternal region of the prothorax is the *prosternum*. In the family Tipulidae the sclerites of the pronotum are usually small and insignificant, being encroached upon by the sclerites of the mesothorax. In some exotic genera, such as the tropicopolitan genus Styringomyia, the prothorax is large and of a generalized structure. In entomological literature the pronotum is usually spoken of as the "neck" or the "collare."

*The mesothorax.*— The mesothorax is the principal region of the thorax in the Tipulidae. The mesonotum, or upper part, is divided into two sclerites, which are again divided so as to appear as four — the prescutum, the scutum, the scutellum, and the postnotum.

The *prescutum* is the anterior, or first, subdivision. In crane-flies it is the largest single region of the thorax, lying behind the pronotum and before the transverse, or V-shaped, suture. It may be very flat and depressed, as in the South African genus Platylimnobia, or very high and gibbous, as in *Dicranomyia globithorax*, *D. gibbera*, and other species; or it may jut far cephalad over the pronotum, as in Conosia and in many species of Trentepohlia. In the subgenus Conorhipidia of the genus Rhipidia, which includes two species from tropical America, the prescutum is elevated into a high conical point, which is very remarkable but is suggested in other species of the same genus, as, for instance, *Rhipidia domestica*. The prescutum is usually striped in various ways, a common pattern being three stripes, one in the middle and two shorter ones on the sides. The spaces between these stripes often bear setigerous punctures, with setae of various forms and sizes. In many genera the prescutum bears two shiny dots, called *tuberculate pits* (fig. 126, B). In certain groups,

as in many species of Limnophila and in the eriopterine series allied to Gonomyia (Gonomyia, Rhabdomastix, and other genera), these pits lie one on either side of the median line of the prescutum, at the extreme cephalic margin; in other groups, as in the eriopterine series allied to Erioptera (Erioptera, *sens. str.*, Empeda, and other genera), they are found on the dorsum of the prescutum, about midlength of the segment. These pits are the double, or paired, dots of Osten Sacken.

The *pseudosutural foveae* (fig. 126, B) are prominent depressions on the sides of the prescutum, in front, lying just above the anterior spiracles,

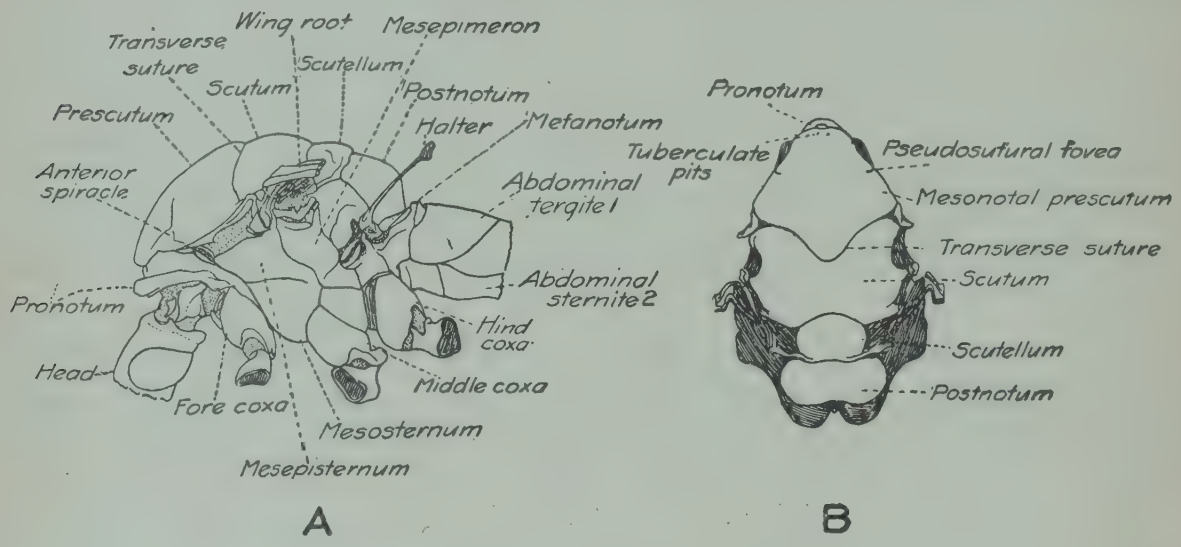


FIG. 126. THORAX OF TIPULA

A, Lateral aspect; B, dorsal aspect. Adapted from Snodgrass

usually in the area before the ends of the short lateral stripes and at the sides of the longer median stripe. These structures have been called the *humeral pits.*

The *scutum* is the second subdivision of the mesonotum. It lies just behind the V-shaped suture and is usually divided into two lateral lobes by a shallow median depression.

The *scutellum* is the third subdivision of the mesonotum. It is a small transverse segment, lying just behind the lobes of the scutum and before the postnotum.

The *postnotum* is the fourth and last subdivision of the mesonotum. It is a large and prominent sclerite situated behind the scutellum, appearing

almost vertical in position. The dorsal part of the postnotum lies between the halteres, and the lateral part between the wings and the scutellum in front and the halteres and the metapleura behind. This region is often erroneously considered as being the metanotum.

The *pleuron* of the mesothorax (fig. 126, A) consists of the mesepisternum and the mesepimeron. The *mesepisternum* is the plate making up the anterior part of the pleuron. It is bounded caudad by the mesepimeron and ventrad by the mesosternum. Its dorso-cephalic angle is close to the mesothoracic spiracle. The *mesepimeron* is the plate making up the posterior part of the pleuron. It is a long sclerite, lying underneath the wing base and bordered behind by the mesonotal postnotum and the metepisternum.

The *sternum* of the mesothorax is usually prominent, lying beneath the pleura and bearing the middle legs.

The mesothorax bears the wings of the insect, as well as the middle legs. The details of the wing venation are discussed under a separate caption (page 860). The wings are always present in crane-flies, but they are very tiny and reduced in the genus Chionea, and in many genera and species they are so reduced as to be useless for flight. This atrophy of the wing may consist of a reduction in width only, the length being unaffected and the organ taking on a straplike appearance (as in *Tipula pribilofensis*); or there may be a reduction in both the length and the width, the wing in extreme cases (such as *Tipula chionoides*, Platylimnobia, and others) being a mere pad which is shorter than the halteres. As a result of the distortion of the wing shape there is a corresponding reduction and atrophy of the venation. In the northeastern United States and eastern Canada, all the crane-flies are full-winged except the nearly wingless Chionea, mentioned above.

The wing surface is usually provided with a microscopic pubescence, to which are due many of the opalescent reflections in crane-flies (as in Antocha, Dicranoptycha, and other genera). In addition to this microscopic pubescence there is also found, in many scattered groups of genera, a strong pubescence, which is apparent with a hand lens. The writer regards the retention of this coarse pubescence as being a primitive character. Its nature varies. In some genera it covers the whole surface of the wing — as in Ormosia, Ula, and Ulomorpha; in many species it is confined to certain of the apical cells of the wings — as in *Dicranomyia*

*pubipennis*, *Erioptera* (*Empeda*) *pubescens*, *Gnophomyia luctuosa*, species of Adelphomyia, the subgenus Lasiomastix of Limnophila, Bittacomorphella, certain Ptychoptera, and some species of Dolichopeza (Trichodolichopeza), Tipula (Trichotipula, Cinctotipula), and so on. In most crane-flies the wing veins likewise bear long hairs, which in some genera, such as Molophilus, are very long; in some species, however, the hairs are so short as to be scarcely noticeable.

*The metathorax.*— The only part of the metanotum, or dorsal sclerite of the metathorax, which is visible is the postnotum. This appears as a narrow, transverse sclerite between the mesonotal postnotum and the first segment of the abdomen. The pleural sclerites consist of the *metepisternum*, a very small sclerite between the metathoracic spiracle and the hind coxae, and the *metepimeron*, a small sclerite behind the halteres.

The metathorax bears the hind legs and the *halteres*, or *balancers*. The halteres are usually considered as being reduced hind wings, and serve an important function in flight. They lie just behind the wings and are of various shapes, in some species (as *Dicranomyia halterata* and *Gonomyia filicauda*, for example) being very long and slender and in other cases being short with prominent swollen knobs. In some groups with reduced wings (such as Platylimnobia) the halteres also are reduced and straplike. The halteres are retained even when the wings have been practically lost, as shown by the genus Chionea.

*The legs*

The legs of crane-flies are as a rule excessively elongated, which gives to the group all or almost all of its common names — *crane-fly* (from a comparison with the crane), *daddy longlegs* (the British name for the group), and so on. The leg is made up of nine segments, designated, respectively, from the body outward, as the *coxa*, the *trochanter*, the *femur*, the *tibia*, and the five *tarsal segments*.

*The coxa.*— The coxa is the enlarged basal segment of the leg, that of the fore leg being called the fore coxa, precoxa, or procoxa, and those of the middle and hind legs having the corresponding prefixes. In the groups with great powers of flight (Megistocera, Trentepohlia, and others) the coxae are very small, while in the species with reduced wings and consequent need of walking (as in the genera Platylimnobia, Chionea,

and others) they are very large and powerful. The coxae are often provided with a dense covering of long silky hairs.

*The trochanter.*— The second segment of the leg, called the trochanter, lies between the coxa and the femur and serves as a pivot between these two major segments. In Dicranoptycha, the distal margin is armed with a sharp blackened tooth which is directed inward.

*The femur.*— The femur is the third segment of the leg, corresponding to the thigh of higher animals. It is the largest and most powerful single element of the leg, being in many cases greatly elongated and

FIG. 127. FEET OF CRANE-FLIES

A, *Limnobia indigena*, male, last tarsal segment and claw. B, *Dicranomyia morioides*, male, last tarsal segment and claw. C, *Rhabdomastix flava*, male, last two segments and claw

incrassated. In some groups (as Ctenacroscelis, for example) it bears a comb of approximated spines near the distal end. In other genera, especially in Trentepohlia, the femur is often armed with groups or rows of stiff bristles or short spines, which furnish valuable specific characters.

*The tibia.*— The tibia is the fourth segment of the leg, situated between the femur and the first (metatarsal) segment of the tarsus. Next to the femur it is the longest single element of the leg. In many groups a pair of spines, or spurs, are borne at the tip, called the *tibial spurs*, and these

are of great importance in classification. These spurs are lacking in the tribes Limnobiini, Antochini, and Eriopterini, but are present in the remainder of the Tipulidae tho in some cases they are so small as to require a low-powered microscope for their detection.

*The tarsal segments.*— The tarsus, or foot of the fly, is made up of the terminal five segments. The first of these segments is the longest and is called the *metatarsus.* The remaining segments gradually decrease in length to the last, which bears the *claws*, or *ungues*, and, when it is present, the *empodium* between the claws. In Bittacomorpha the metatarsus is swollen and bladder-like. In one species of Lecteria the metatarsus bears a group of three stout spines at the extreme base. The claws of most crane-flies are quite smooth (fig. 127, C, Rhabdomastix), but those of species of the tribe Limnobiini have teeth on the ventral side (fig. 127, A, Limnobia; fig. 127, B, Dicranomyia). A similar condition is found in certain Dolichopezini, such as Brachypremna and Tanypremna, but not in Megistocera.

*The transverse suture*

The transverse suture is considered one of the important characters for use in distinguishing the Tipulidae from related families of flies, such as the Dixidae, the Mycetophilidae, and others. It is in the shape of a low V, and separates the mesonotal prescutum from the scutum.

*The wings and their venation*

The wings of crane-flies, with their remarkably constant venation and pattern, furnish the easiest and best characters for recognition of the various forms. In the great majority of cases a glance at the wing is sufficient for the determination of the species, and it is for this reason that considerable emphasis is here placed on these organs. This paper discusses only in a rather elementary way the essentials of the wing venation, but Needham (1908) has made a critical survey of the character in all the genera of the Tipulidae known at the time his work was prepared, and his paper is absolutely essential to the student of this group of insects.

The wing is made up of a series of longitudinal veins running from the base to the outer margin and bound together at various points by cross-veins and by deflections of the longitudinal veins which produce

strong fusions at these places. The more specialized forms have an unusually strong series of cross-veins and deflections running transversely or obliquely across the wing at about two-thirds its length and generally in line with the ending of the radial sector and the inner end of the cell *1st* $M_2$ (discal). This strong fusion is called the *cord*, and a glance at almost any wing will enable one to pick it out immediately. The genus Pedicia (Plate XLII, 175) has the elements of the cord in almost perfect alinement, but very oblique, and here the principal parts entering in are the basal deflection of $Cu_1$, the basal deflection of $M_{1+2}$, and the *r-m* cross-vein; in most crane-flies the deflection of $R_{1+5}$ adds another strong element to the cord, while in many genera (as Antocha, Plate XXXIII, 48, and Teucholabis, Plate XXXIII, 52 and 53) the radial cross-vein is so placed as to become still another strong element. Very often the radial sector enters in as the part nearest to the main radial vein ($R_1$), and here the stress falls either on the sector or on $R_{2+3}$, or on both. As has been pointed out by Needham, in many species the closed cell of the wing (*1st* $M_2$) is swung directly across the path of the cord, interrupting it like a ring on a line; the medial cross-vein and the outer deflection of $M_3$ are quite necessary to complete this ring, and they are always present in such cases. It is only when the inner end of the closed cell gets into alinement with the other elements of the cord, so that the ring formed by the cell is no longer needed to strengthen the wing disk, that the medial cross-vein is lost by atrophy.

*The longitudinal veins.*— There are six or seven longitudinal veins, named, respectively, from the front margin backward, the *costa*, the *subcosta*, the *radius*, the *media*, the *cubitus*, and the *anal veins*.

The *costa* (*C*, fig. 128, A) forms the anterior margin of the wing. It is usually much thickened, but thins out before reaching the wing apex. It is strongly united with the vein beneath it, the subcosta, by the humeral cross-vein at the base of the wing. More distally other veins end in the costa, such as $Sc_1$, $R_1$, and usually other elements of the radial field.

The *subcosta* (*Sc*, fig. 128, A), a weak vein lying between the costa and the radius, is often difficult to detect due to foldings and flexings of this part of the wing. In generalized forms it is forked, the anterior branch, $Sc_1$, going to the costa, and the posterior branch, $Sc_2$ (the subcostal cross-vein of the older authors), connecting with $R_1$. In the subfamily Limnobiinae, $Sc_1$ is usually present, and $Sc_2$ may be close to its tip as in

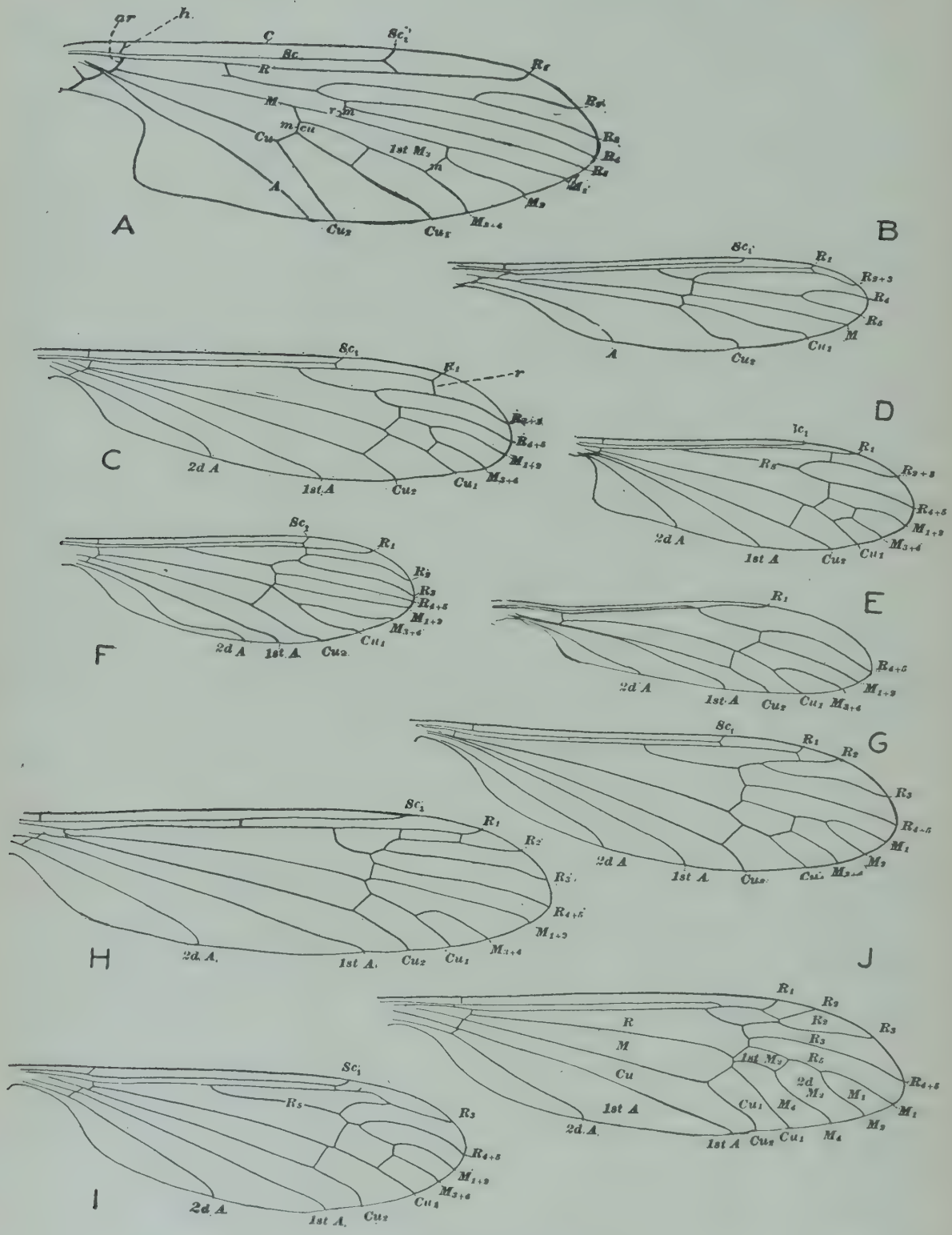


FIG. 128. WING VENATION

A, *Protoplasa fitchii*. B, *Bittacomorpha clavipes*. C, *Dicranomyia pubipennis*. D, *Antocha saxicola*. E, *Toxorhina muliebris*. F, *Erioptera septemtrionis*. G, *Limnophila subcostata*. H, *Dicranota rivularis*. I, *Liogma nodicornis*. J, *Tipula unifasciata*

most Limnophilini (Plates XXXVIII–XLI), or it may tend to retreat proximad toward the base of the wing as in many Eriopterini (Plates XXXIV–XXXVII), or it may be very far removed from the tip so that it lies before the base of the sector (as in the tribe Pediciini, Plates XLI, XLII, and in the genus Ula, Plate XLI, 164). In some Antochini it is apparently lost by atrophy. In the subfamily Tipulinae only the more generalized species retain $Sc_1$ (Plate XLIII, 188 and 189), but $Sc_2$ is present and is bent strongly into $R_1$ at its tip, thus forming a good subfamily character.

The *radius* (*R*, fig. 128, A) is the strongest vein of the wing, and, with its sector, one of the most plastic. $R_1$ runs straight to the wing margin, but usually at about midlength of the wing it forks, sending off the radial sector (*Rs*). This is primitively twice forked, being forked and the branches forked again, dichotomously. These branches of the sector are numbered from 2 to 5, the upper fork carrying with it $R_2$ and $R_3$ and the lower fork carrying with it $R_4$ and $R_5$. The full complement of branches of the radial sector is found only in the Tanyderidae (Plate XXX, 1). In the Ptychopteridae (Plate XXX, 2–4) the upper fork, $R_{2+3}$, is fused to the margin; in the Tipulidae (Plates XXX–XLVIII) it is almost always the lower of the dichotomous forkings, $R_{4+5}$, that is fused to the margin.

The various ways in which the full complement of veins has been lost, by the fusing together of adjacent veins or else by the atrophy or dropping out of one or more of the branches, may be here discussed. In the Cylindrotominae (Plate XXX, 5–8) the appearance suggests the fusion of the upper fork of the sector ($R_{2+3}$) with $R_1$, forming a long, backward fusion of $R_{1+2+3}$ from the wing margin. As suggested by the author in an earlier paper (Alexander, 1914 b: 604–605) and later proved by the discovery of the Oriental genus Stibadocera Enderlein (Alexander, 1915 c: 178–179), the loss of these veins is by atrophy rather than by fusion, and the vein that simulates $R_{1+2+3}$ is, in reality, $R_3$ alone and corresponds exactly to this vein in other tribes of crane-flies. In the subgenus Leiponeura of the genus Gonomyia (Plate XXXVI, 86–88), the vein $R_{2+3}$ is fused to the wing margin, or, possibly, $R_3$ is atrophied after the fusion has proceeded almost to the margin. In the more generalized species of Gonomyia (Plate XXXVI, 89 and 90), the fork of $R_{2+3}$ is

relatively deep, but it gradually becomes shallower until in such forms as *G. sulphurella* (Plate XXXVI, 91) it is very small and only a step removed from the condition obtaining in the subgenus Leiponeura. The venation in the genus Cladolipes, of the tribe Hexatomini, is similar. The genus Paratropeza of the tribe Antochini is the only member of that tribe with $R_2$ and $R_3$ separate at the wing margin, and in keys to the Tipulidae this genus runs down to the Eriopterini; the species are all exotic and are evidently the most generalized members of this aberrant tribe. In a few species of Gonomyia related to *G. blanda* (Plate XXXVI, 89 and 90), $R_2$ is very close to $R_1$ at the wing margin, in some cases being actually fused with it; this is likewise the condition in the Neotropical group Psaronius, where the fusion is most emphatic. The fork of $R_{2+3}$ is often very deep, this cell being in many instances sessile or with $R_2$ even retreated back onto the radial sector (as in Molophilus, Plate XXXIV, 65–70; Tricyphona, Plate XLII, 178–185; *Limnophila emmelina*, Plate XL, 151; Rhaphidolabis, Plate XLI, 172–174), in which cases the anterior branch of the sector is simple and the posterior branch is forked, as in the Ptychopteridae already mentioned. These shiftings of the elements of the fork of the radial sector have been critically studied by Needham (1908). The radial cross-vein apparently is lost only by atrophy; the Cylindrotominae, discussed above, which appear to lose this vein by the fusion upon it of adjacent veins, in reality have it present and elongated, but simulating a section of vein $R_1$. In Eurhamphidia and Rhampholimnobia, of the East Indies, the fork of the radial sector occurs far beyond the line of the cord, while in most other crane-flies it is before or at this line. The radial-medial cross-vein (*r-m*) is usually present, but if lacking it is accounted for, apparently, only by the fusion of $R_{4+5}$ on $M_{1+2}$ (fig. 128, 1); this fusion may be slight or extensive, and occurs in scattered genera in all the subfamilies of the Tipulidae. The radial-medial cross-vein lies distad of the medial cross-vein in Conosia and in some species of Rhamphidia. In many Dolichopezini (Plate XLIII, 186 and 187), Tipulini (Plate XLVIII, 247 and 248), and Cylindrotominae (Plate XXX, 5–8), the whole tip of $R_2$ is atrophied. In the remarkable genus Toxorhina (Plate XXXIII, 45 and 46), the radial sector is unbranched but the branch that persists is undoubtedly $R_{4+5}$ alone, $R_{2+3}$ having retreated back toward

the base of the sector and finally being lost by atrophy or by fusion with $R_1$; the exotic genus Ceratocheilus shows this intermediate condition very remarkably, and indicates clearly the manner in which this extreme reduction of the sector in Toxorhina was brought about.

The *media* ($M$, fig. 128, A), or medial vein, like the radial sector, in the hypothetical type of an insect wing is twice dichotomously forked, the closed cell, *1st* $M_2$, lying in the first fork. There are no known crane-flies that show this condition except the doubtful fossil genus Rhabdinobrochus, which is apparently based on an abnormal and imperfectly preserved specimen, and occasionally freak specimens of Tipula which indicate this condition by spurs of varying length. These specimens show that the single posterior branch of the media which persists is $M_4$, the spur always lying on the cephalic side and representing the atrophied $M_3$. Comstock (1918:349, fig. 360) has interpreted the venation of *Protoplasa fitchii* as showing all four branches of media, $M_4$ being fused with $Cu_1$ distally. That this is not the true interpretation is indicated by a study of the other species of Protoplasa. The vein in cell $M_3$ which Comstock interprets as being the downward deflection of $M_4$ is a supernumerary cross-vein. In this remarkable family of flies, such cross-veins are very often found in different cells of the wings. That the presence of a vein in cell $M_3$ is a specific character only is shown by the fact that it is lacking in the related *Protoplasa vipio* O. S. $M_1$ and $M_2$, comprising the anterior fork of the vein, are either separate or fused at the wing margin; such genera as Limnophila (Plates XXXVIII–XL) show a perfect succession, from deep forks as in the exotic *Limnophila epiphragmoides* (Alexander, 1913 b:543), thru less deep forks as in *L. montana* (Plate XL, 148), to *L. brevifurca* (Plate XXXVIII, 125), which has a very shallow fork that is sometimes fused clear to the wing margin, and further to the numerous species of the genus (Plate XL, 150–157) in which there is a permanent and constant fusion between these veins extending entirely to the wing margin and obliterating the cell $M_1$. In all except the most generalized species, including nearly all of the Limnobiinae, the medial-cubital cross-vein (*m-cu*) is obliterated by the fusion of $M_{3+4}$ with the upward deflection of $Cu_1$; this fusion may be short or long, and is discussed in connection with the cubitus. After breaking away from the cubitus, $M_3$ generally runs free to the wing margin, but in some cases (as in Styringomyia and Phalacrocera, Plate XXX, 8 and 9) it

unites with $M_{1+2}$ for a short distance, obliterating the medial cross-vein. In some genera — Bittacomorpha (Plate XXX, 3), Bittacomorphella (Plate XXX, 4), Hexatoma (Plate XXXVII, 112), Diotrepha, and many species of Trentepohlia — but one branch of the media reaches the wing margin, and in these cases the posterior branch has either fused with the cubitus (as in Hexatoma) and reaches the margin by this fusion, or has been lost by atrophy. Needham (1908:227–229) believes the posterior branch of the media is lost only by atrophy, and undoubtedly this is true in most instances; the series of Polymera, however, a tropical, American genus studied by the author (Alexander, 1913 b:526–535), showed an interesting condition indicating that the veins may be united by fusion, and similar conditions may exist in the genus Rhaphidolabis and in the South African species *Gonomyia brevifurca*. The entire end of $M_3$ is lost by atrophy in four known species of Dicranomyia, one of these being *D. whartoni* (Plate XXXI, 15). The cell *1st* $M_2$ (discal) is in many cases opened by the atrophy of part of $M_3$, leaving the tip of $M_3$ attached to the medial cross-vein (as in Ormosia, Plate XXXIV, 59–64, and in Gonomyia, Plate XXXVI, 92 and 93); in other cases it is the medial cross-vein (*m*) that is atrophied, opening the cell (as in Dicranomyia, Plate XXXI, 14 and 16, in Cryptolabis, Plate XXXVII, 101, and in many genera of the Pediciini, Plate XLI, 172–174).

The *cubitus* (*Cu*, fig. 128, A), lying between the media and the anal veins, is the most constant and, after the radius, the most powerful vein of the wing. There are always two branches, which are never lost. At the fork, the anterior branch, $Cu_1$, is directed strongly forward, so that in all but the most generalized forms it simulates a cross-vein and from its conspicuous size it has long been termed the *great cross-vein*; this deflection is the basal deflection of $Cu_1$ of the Comstock-Needham system, and the *pars ascendens* of Bergroth. In the more generalized groups, such as Tanyderidae (Plate XXX, 1), Ptychopteridae (Plate XXX, 2–4), a very few Limnobiinae — as some species of Tricyphona (Plate XLII, 184 and 185) — and many of the Tipulinae (Plate XLIII, 195–197), the medial-cubital cross-vein (*m-cu*) is persistent, but in the great majority of cases it is lost by the fusion of $Cu_1$ and $M_{3+4}$. As already stated, this fusion may be very short — merely a point of contact (punctiform), as in most species of Tipula (Plate XLVI, 222) — or it may be subequal in length to the cell *1st* $M_2$, the deflection of $Cu_1$ entering the media at

its fork and breaking away from $M_3$ at the distal end of the cell; this long fusion with $M_3$ is the rule in the subfamily Limnobiinae, but is very unusual in the Tipulinae, the South African genus Leptotipula being almost the only instance known. In some groups the deflection lies far before the fork of the media, as in the transient fusions of Nephrotoma (Plate XLIV, 198 and 202) and Dolichopeza (Plate XLIII, 187) or the longer fusions of many Gonomyia (Plate XXXVI, 89 and 90) and other genera. In the highly specialized condition obtaining in Orimarga and even more accentuated in the tropical-American genus Diotrepha, the deflection of $Cu_1$ is retreated far toward the wing base, so that in the latter genus the fusion of $Cu_1$ with $M$ is about half the length of the entire wing. On the other hand, $Cu_1$ may unite with $M_3$ far out toward the tip of the wing, (as in Trichocera, Plate XLI, 165 and 166), so that $Cu_1$ extends beyond $M$ and is connected with it by the *m-cu* cross-vein, which here runs longitudinally and simulates a section of one of the longitudinal veins. In the great majority of crane-flies, the fork of the cubitus is so deep that the branch $Cu_2$ is longer than the deflected part of $Cu_1$; in some species of Limnophila (Plate XXXVIII, 113), however, and also and especially in the tribe Hexatomini (Plate XXXVII, 104 and 105), the condition is usually reversed and it is $Cu_2$ that is the shorter element of the fork. $Cu_2$ is usually free at the wing margin, but in most Old World species of Trentepohlia and in one species of Dicranomyia it is fused with the first anal vein for a varying distance back from the tip.

The *anal veins* (*1st A*, *2d A*, fig. 128) comprise in the generalized wing three simple veins, as apparently shown in the fossil genus Cladoneura; a single anal vein is found in the Ptychopteridae and in most of the Tanyderidae, and there are two in all the Tipulidae and in the fossil tanyderid genus Etoptychoptera Handlirsch. The anal veins are simple in all native forms; the second one is forked in the South African genus Podoneura, in some species of Styringomyia, and in abnormal specimens of Helobia. As indicated by Needham (1908), if the second anal vein found in Helobia (Plate XXXVII, 98) and that in Trichocera (Plate XLI, 165) were united, the condition would be remarkably like what is found in Podoneura, and the condition in these genera may have been brought about by the loss of the anterior branch of the fork in Trichocera and the posterior branch in Helobia. In the Tipulini and some other tribes there is a strong vein lying close beneath *Cu* and often quite removed

from it. This probably represents the first anal vein in these species, in which case all three anal veins would be accounted for.

*The cross-veins.* — The usual cross-veins of the wing have been indicated, for the most part, in the foregoing discussion of the longitudinal veins. The humeral cross-vein (*h*) is almost always present and forms a strong union between *C* and *Sc* near the wing base; it is of little systematic importance. The radial cross-vein (*r*) lies entirely in the radial field, and connects $R_1$ with either $R_2$ or $R_{2+3}$, or it may lie exactly at the fork of the last-named vein. The radial-medial (*r-m*) cross-vein connects either $R_{4+5}$ with $M_{1+2}$ as in most crane-flies, or $R_5$ with $M_{1+2}$ as in Molophilus (Plate XXXIV, 65–70), or *Rs* with $M_{1+2}$ as in *Tricyphona kuwanai* of Japan and in the genus Rhampholimnobia discussed above. The medial cross-vein (*m*) lies entirely in the medial field and connects either $M_2$ or $M_{1+2}$ with $M_{3+4}$. The medial-cubital cross-vein (*m–cu*) connects either *M* or $M_{3+4}$ with $Cu_1$. The arculus (*ar*) is a strong cross-vein connecting *M* with *Cu* at the base of the wing.

Supernumerary cross-veins and spurs are frequently found in crane-flies and furnish convenient characters for defining genera, subgenera, and species. In *Tanypremna regina*, of the Colombian Andes, there is an abundance of cross-veins and spurs in the basal cells of the wings; in the related species *Tanypremna columbiana* there is a single strong cross-vein in cell *M*. These supernumerary cross-veins are very constant in their occurrence and position, and may be found in almost any cell of the wing. Needham (1908:220) drew a primitive crane-fly wing and indicated on it all the supernumerary cross-veins that are known to occur in the group, and the composite resulting was remarkably like the wing of a neuropteroid scorpion fly, thus providing additional confirmation for the belief that the Panorpidae or some closely allied group gave rise to the dipterous line of evolution. Epiphragma (Plate XLI, 158) has the cross-vein in cell *C*; Geranomyia (Plate XXXI, 10–13) and many Rhipidia in cell *Sc*; Helobia (Plate XXXVII, 98) and Dicranophragma (Plate XXXIX, 139) in cell $R_2$; Ephelia (Plate XXXIX, 137 and 138) and Idioptera (Plate XXXVIII, 115) in cell *M*; Dicranota (Plate XLI, 167–169) in cell $R_1$, alongside of the *r* cross-vein; Discobola (Plate XXXII, 41) in the first anal cell, forming a strong union between the two anal veins; and so on in great variety. Strong spurs are frequently found at the origin of the radial sector (Plate XXXVIII, 115 and 116), or in a

few cases in other parts of the wing, as in Hoplolabis (Plate XXXV, 83), where a strong spur juts into cell *1st* $M_2$ from its outer end.

Adventitious cross-veins, or veins which are inconstant and of sporadic occurrence within a species, being in some cases present in one and absent in the other of the two wings of a single individual, are rather frequent in the Tipulidae, the most notable cases being the genus Cladura (Plate XXXVII, 102) as noted by Alexander and Leonard (1912), and the species *Tricyphona inconstans* (Plate XLII, 177) as noted by Johnson (1901).

*The cells.*— The cells of the wing take their names respectively from the veins lying immediately before or above them; in the case of fused veins the cell takes its name from the last element of the fusion. Thus the cell behind vein $R_3$ is cell $R_3$, that behind vein $M_1$ is cell $M_1$, that behind vein $R_{4+5}$ is cell $R_5$, and so on (fig. 128, J). When the cells of a field are cut by cross-veins, either primary such as *r* and *m* or supernumerary, the proximal cell is the first and the distal cell is the second. Thus in many crane-flies the discal cell is present, being cut off by the *m* cross-vein at its outer end; and since both cells lie behind vein $M_{1+2}$, both are cell $M_2$, the proximal cell (discal) thus becoming *1st* $M_2$ and the outer cell becoming *2d* $M_2$. The same thing is true of the cell $R_1$, which in some cases (as in Dicranota, Plate XLI, 167–169) is divided into three cells, numbered outward from the proximal (*1st* $R_1$) to the distal (*3d* $R_1$). In most cases the wing cells lying proximad of the arculus are so small and reduced that they cannot be readily homologized; but in the tropical-American genus Peripheroptera they attain a remarkable development, occupying in the males of some species from one-third to one-half of the entire wing length. The anal angle of the wing is variously developed, being usually prominent in the family Tanyderidae (Plate XXX, 1), the genus Antocha (Plate XXXIII, 48), and the subgenus Sacandaga of the genus Rhabdomastix (Plate XXXVI, 97), and on the other hand being lacking or nearly so in some exotic Limnobiini, such as Thrypticomyia and the males of Peripheroptera.

*The stigma.*— The stigma is a dark spot or area usually situated near the end of vein $R_1$ and often bisected by the radial cross-vein. It may be either present or lacking in the various species of a genus, and in some cases is very large and pubescent, as in the males of the genus Empedomorpha Alexander.

*The abdomen*

The abdomen, the third and last region of the body, lies behind the thorax and is attached to the caudal parts of the metathorax. It is composed of nine apparent segments, or annuli, numbered from the basal (first) to the terminal (ninth). Each of these segments consists of three regions — a dorsal sclerite, the *tergite*; a ventral sclerite, the *sternite*; and a lateral region on either side, the *pleurites*, these being either integumentary or chitinized. The abdominal spiracles are located in this pleural conjunctiva. There is but little modification of the general type in the various groups of crane-flies.

The first segment is very short and appears as a narrow ring closely attached to the metathorax; the second is the longest of the segments; the remaining segments are subequal in size, or, in the male sex especially, shortened and crowded toward the end of the abdomen. In many species of Tipulinae there are present on the abdominal segments rectangular areas of impressed punctures on either side of the median line, which on the second tergite are about midlength of the sclerite and on the succeeding tergites are on the basal part; often there are smaller areas of punctures nearer the caudal margin of the sclerites. These areas are usually present on the sternites as well as on the tergites. The sexual organs are borne at the end of the abdomen in both sexes.

*The male hypopygium.* — The hypopygium, or propygium, of the male sex is of extreme importance in the determination of species. In many groups and genera (Gonomyia, Molophilus, Tipula, and others) it is almost impossible to identify the species without considering the details of structure of the male genitalia, and in these groups the hypopygium is of paramount importance in specific determination.

The structure of the hypopygium is relatively uniform and homologous thruout the crane-fly series. The organ has been discussed in considerable detail by previous authors, especially by Snodgrass (1904), whose terminology is adopted in this paper. The European authors still adhere largely to the cumbersome terminology of Westhoff (1882).

In the generalized species the hypopygium shows but little complexity and enlargement, the terminal segments of the abdomen being of approximately the same size and diameter as the preceding segments. In the specialized species of many genera (Gonomyia, Limnophila, Tipula,

and others), the hypopygium is enlarged and complicated in structure, the enlargement often involving the terminal two or three segments. The modifications of the eighth and ninth segments are almost inconceivable in their variety, and only the more important types can be mentioned here.

The Tipulinae: In the tipuline forms the pleura are intimately attached to the sternites, and their appendages lie parallel to each other,

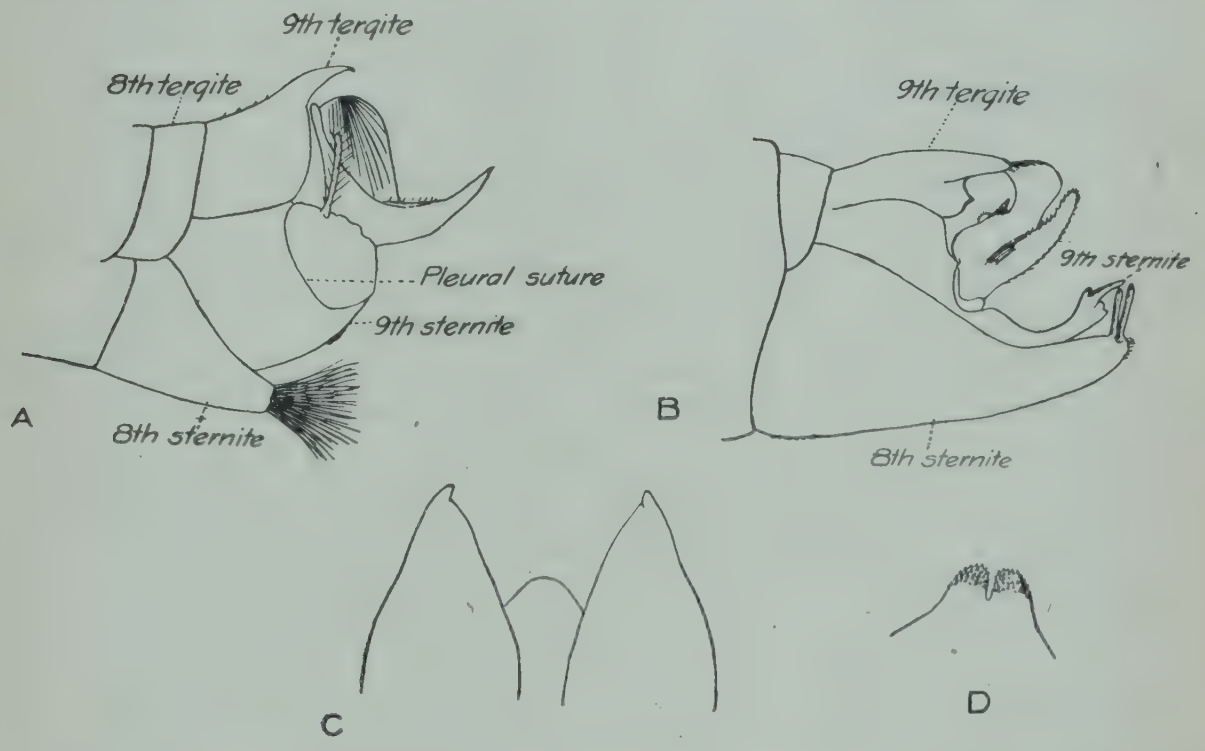


FIG. 129. MALE HYPOPYGIUM, TIPULINAE

A, *Tipula monticola*, lateral aspect. B, *T. parshleyi*, lateral aspect. C, *T. monticola*, ninth tergite, dorsal aspect. D, *T. sulphurea*, ninth tergite, dorsal aspect

work longitudinally, and act as claspers by jutting into the notch of the ninth tergite.

The ninth tergite (fig. 129, C and D) is the terminal dorsal plate of the abdomen. It is of various shapes, but usually rectangular, and may be very large or correspondingly reduced. The caudal margin is variously modified (Plates XLIX–LII), being in some cases nearly straight across and in others notched by V- or U-shaped incisions, with the lateral lobes often produced into long-extending arms, and the appendages of the ninth pleurite jutting into the notch in a position of rest. In some cases the

caudal margin is produced into a strong median lobe (Plate L, 287), or into two slender lobes (Plate XLIX, 271 and 272), one on either side of the median line. The writer regards the ninth tergite as offering the surest and easiest characters for identifying the species of Tipula, and its various forms are accordingly illustrated in this paper.

The ninth sternite may be either prominent or insignificant. It bears on its caudal part the ninth pleurites, or pleural region. In primitive forms the pleurites are distinct, being cut off by the *pleural suture* (fig. 129, A); in other forms the suture is obliterated to a greater or less degree and the pleural region is thus immovably attached to the sternite. In very many Tipulinae (as in most species of Nephrotoma and many species of Tipula), the pleural suture is represented only by a short, curved impression on the ventral side of the fused ninth sterno-pleurite. In the genus Longurio the ninth sterno-pleurite is exceedingly elongated, the pleural region being situated at the caudal end and bearing at its apex the pleural appendages, which, in a position of rest, lie in the dorsal concavity of the elongate sterno-pleurite. In some species — *Tipula parshleyi* (fig. 129, B, and Plate LV, 354), *T. trinidadensis*, *T. macrosterna*, *T. gladiator*, and others — it is the eighth sternite that is so greatly enlarged, the ninth sternite being comparatively small and often lying in the dorsal concavity of the eighth sternite. The ninth sternite is usually more or less incised on the mid-ventral line by a deep notch, which in some cases seems to bisect it; such deep notches are spoken of as *profound incisions*.

The only paired element of the hypopygium consists of the ninth pleurites, there being one pleurite on either side of the organ. Usually the pleurites are small and oval, but in some cases they are greatly produced, as in *Tipula macrolabis* and *T. macrolaboides* (Plate LIII, 322 and 323); in other species they are curiously twisted and semi-coiled, as in *T. streptocera;* while in many species an intermediate condition is found in which the pleurite is produced in a moderate degree only (as in *T. loewiana*, *T. mandan*, and others). The pleural appendages are usually two in number. The outer one is more or less fleshy and is of various shapes and sizes in the different groups. In the genus Nephrotoma it is broadly oval to elongate-oval and usually pointed, in many species the tips being greatly produced and attenuated. In the genus Tipula it may be very tiny, cylindrical, and tending to be reduced, as in the

*bicornis* group (*Tipula parshleyi*, *T. morrisoni*, *T. bicornis*, *T. megaura*, *T. johnsoniana*); moderate in size and more or less cylindrical, as in the *valida* group (*T. valida*, *T. hirsuta*) and the *umbrosa* group (*T. umbrosa*, *T. monticola*, *T. triton*, *T. mingwe*, *T. tuscarora*); or broad, rectangular, and very flattened, as in the *oleracea* group (*T. perlongipes*, *T. kennicotti*, *T. sulphurea*) and the *tephrocephala* group (*T. tephrocephala*, *T. cayuga*). The inner pleural appendage varies in shape, but usually it has a heavily chitinized, split apex jutting cephalad into the notch of the ninth tergite.

The penis guard and the gonapophyses vary in size and shape. In some species, as *Tipula tuscarora*, they are small and shaped like a trident; in other species (*T. triton*, *T. johnsoniana*) the gonapophyses are very large and prominent, and subtend the penis guard. The central vesicles from which the penis arises are often very large. In many species the penis is very long and slender, and when exserted is equal to half the length of the entire abdomen.

In many species the eighth sternite is not at all produced and is unarmed (*Tipula angustipennis*, *T. senega*, *T. serta*, *T. perlongipes*, *T. kennicotti*, *T. sulphurea*); in other species it is provided with prominent chitinized spines on either side, which are decussate (*T. tuscarora*, Plate LIII, 328), or with large to small tufts of silvery hairs on either side of the median line, these often surrounding one or two small bristles (*T. monticola*, *T. triton*, *T. mingwe*, *T. submaculata*), or with fleshy lobes (*T. australis*, Plate LIII, 326, *T. umbrosa*, *T. valida*). In the generalized members of the South American *monilifera* group (*T. exilis*, *T. andalgala*, and others) the sternite bears a prominent tripartite appendage.

In several species the ninth tergite is fused with the ninth sterno-pleurite so that the entire ninth segment forms a continuous ring, as in *Tipula ultima* (Plate LIII, 333), *T. perlongipes*, *T. kennicotti*, *T. sulphurea*.

The Limnobiinae: In the limnobiine forms the pleurites are prominent and have their appendages elevated above the level of the ninth sternite and the ninth tergite; these appendages are very often decussate or contiguous, work transversely across the genital chamber, and act as claspers by direct, pincer-like contact. In the genus Geranomyia (fig. 130, A) and others, the ventral pleural appendages are generally soft and fleshy, and the dorsal pleural appendages are sharp, more or less curved, chitinized hooks. In Gonomyia (fig. 130, B) the appendages are very complex in the

specialized forms, and are difficult to homologize even in species that are unquestionably closely related. This condition occurs in several other groups, as in the mycetophilous genus Sciophila and related groups, according to Dr. Johannsen, who has studied the family. In Acyphona and other genera the hypopygium is asymmetrical in relation to the remainder of the abdomen, the ninth abdominal segment being twisted half around. In some limnophiline forms (Phyllolabis, Oromyia, *Limnophila mundoides*) the hypopygium is enlarged and complex, suggesting the condition found in many species of Tipula; in Phyllolabis the eighth

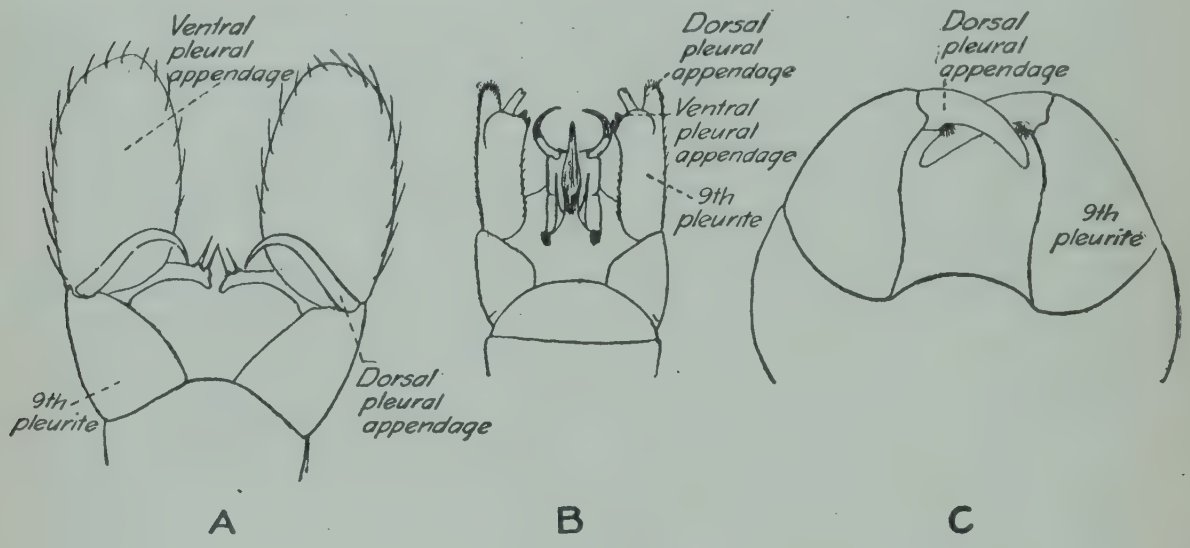


FIG. 130. MALE HYPOPYGIUM, LIMNOBIINAE

A, *Geranomyia rostrata*, dorsal aspect. B, *Gonomyia amazona*, ventral aspect. C, *Chionea primitiva*, dorsal aspect

sternite bears a pale foliaceous appendage, while in Oromyia the ninth sternite is produced into a conspicuous lyriform plate. In Chionea (fig. 130 c), Cladura, and Pterochionea, there is a single powerful pleural appendage on each side.

The normal type of structure in the Limnobiinae consists of short to elongate pleurites, bearing at or near the apices two or three appendages which are usually chitinized and decussate in a position of rest. The penis guard occupies the ventral area of the genital chamber, the anal tube the dorsal area.

*The female hypopygium.*— The female hypopygium, or ovipositor, is characteristic in many species of the Tipulidae. In most cases it consists

of four horny or chitinized pointed valves, which are paired — there being two dorsal (*tergal*) and two ventral (*sternal*) valves. These valves are often acicular and are used for the insertion of the eggs in oviposition. In most species they are curved upward so that the concavity is on the dorsal side, but in the genus Trichocera (fig. 131, A) and some of its near allies the ovipositor bends downward, the concavity being on the ventral side.

As wide a range in structure of this usually homogeneous organ as occurs in the group, is found in the genus Tipula. The tergal valves

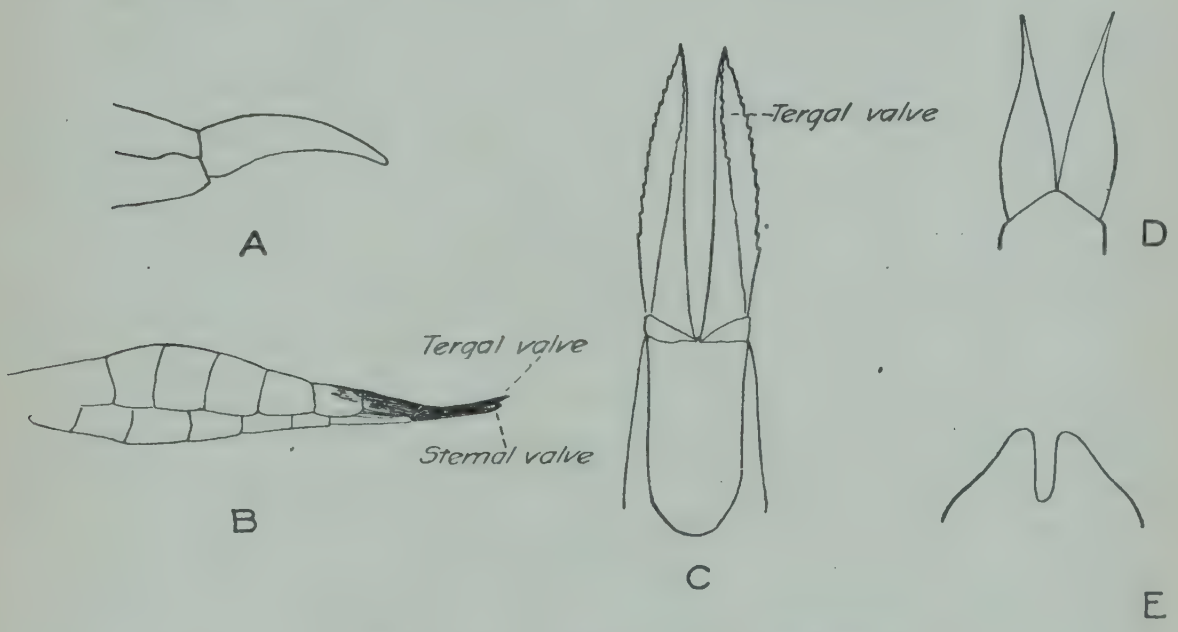


FIG. 131. FEMALE HYPOPYGIUM, OR OVIPOSITOR

A, *Trichocera bimacula*, lateral aspect. B, *Tanyptera frontalis*, lateral aspect. C, *Tipula longiventris*, dorsal aspect. D, *Tipula piliceps*, dorsal aspect. E, *Tipula parshleyi*, dorsal aspect

are usually longer than the sternal valves (fig. 131, C), and both tergal and sternal valves assume a variety of shapes. They are often slender to subacicular; the tergal valves may be sharply serrated on their outer faces, as in many Arctic and North Temperate species — *Tipula arctica*, *T. longiventris* (fig. 131, C), *T. labradorica*, *T. serricauda*; all the valves may be short and fleshy, superficially resembling the male genitalia but being smaller — as in the Cylindrotominae and Styringomyiini, and in *Tipula bicornis*, *T. megaura*, *T. parshleyi* (fig. 131, E), *T. morrisoni*, *T. nobilis*, and other species; all the valves may be short and truncated across their tips but strongly chitinized, as in *Tipula mandan*; or the sternal

valves may be very much reduced, as in *Tipula serricauda*. The ovipositor in Tanyptera (fig. 131, B) is normal, but the terminal abdominal segments are greatly narrowed and produce a saber-like appearance.

### SEXUAL DIMORPHISM

Besides the differences between the two sexes in the shape of the antennal segments, already discussed, there are many other structural differences. In some species the eyes of the female are much smaller than those of the male, and in the latter the eyes may be contiguous (*holoptic*) or approximated. In species with elongated rostra, such as in the genus Geranomyia, the rostrum of the female is often much shorter than that of the male. The legs of the female are in some cases shorter than those of the male. The wings of the females of many species in widely separated tribes are often reduced so as to be incapable of flight; in some forms (Empedomorpha) the stigma of the male is much larger than that of the female; in *Tipula armatipennis* of southern Brazil, the wing of the male is armed with an acute spur above the stigma; many other species have the costal region strongly incrassated; in the genus Peripheroptera, with the greatly enlarged cells before the arculus described elsewhere, these cells are much smaller in the female than in the male, and the anal angle of the wing is more prominent.

Color dimorphism is found in the species of Ctenophora and Tanyptera, the specific limits of which are very poorly understood at present. In at least three eastern-American species of Tipula (*Tipula fuliginosa*, *T. annulicornis*, and *T. taughannock*), the males are light yellow, while the females are from dark brown to brownish black and appear to be very different insects.

As a rule the females are larger than their mates, but in some species (Teucholabis, *Eriocera longicornis*, and others) the male sex is the larger.

### HAUNTS

The various species of Tipulidae are, within rather broad limits, confined to certain definite haunts or ecological situations. Some species are very closely restricted by their habitat, while others occur in a great diversity of situations. There is no crane-fly that can be called cosmopolitan; *Helobia hybrida* is nearly so, ranging, as it does, over most of the New World, the Palaearctic region, and southward into the Oriental

region. *Conosia irrorata* is another wide-ranging species, being found in almost all of eastern Africa, in southern Asia as far north as Japan, and thence eastward to Australia. *Nephrotoma ferruginea*, one of the commonest of the local forms, ranges over the whole North American continent. The majority of species, however, have a very much more restricted range, the crane-fly fauna of eastern America being largely confined to that region, while the crane-flies found west of the Rocky Mountains are almost all distinct from those of eastern America. Natural barriers, such as large bodies of water, deserts, and mountains, serve to limit and restrict the range of the species.

The presence of moisture is almost a necessity in crane-fly development, and consequently the species as adults occur in the vicinity of water, either running, standing, stagnant, permanent, or temporary. No species confined to sandy or arid conditions are known to the writer, the nearest approach being in Helobia, Trimicra, and Empedomorpha. A few typical situations are here outlined and the more constant inhabitants of these haunts listed:

1. Species inhabiting swampy (helophytic) situations: either grass swamps with little woody elements entering in — *Dicranomyia longipennis, Erioptera graphica, E. parva, Stygeropis fuscipennis, Tipula sayi, T. tricolor*; or bush swamps with a certain shrubby element such as Alnus, Spiraea, and the like — *Bittacomorpha clavipes, Ptychoptera rufocincta, Adelphomyia cayuga, Limnophila fasciolata, Rhamphidia mainensis, Tipula dejecta, T. sulphurea, Tricyphona inconstans, T. paludicola.*

2. Species inhabiting wet meadows or grasslands, and found along the (usually) grassy banks of streams not necessarily in deep shade — *Protoplasa fitchii, Geranomyia canadensis, G. rostrata, Antocha saxicola, Toxorhina muliebris, Rhamphidia flavipes, Atarba picticornis, Erioptera chlorophylla, E. straminea, E. vespertina, E. caloptera, E. armata, E. venusta, Gnophomyia tristissima, Gonomyia sacandaga, G. alexanderi, G. sulphurella, G. cognatella, G. subcinerea, G. noveboracensis, G. mathesoni, Rhabdomastix flava, Cryptolabis paradoxa, Epiphragma fascipennis, Limnophila macrocera, L. unica, L. tenuipes, L. recondita, L. imbecilla, L. luteipennis, L. inornata, L. quadrata, L. lenta, L. noveboracensis, Hexatoma megacera, Eriocera fultonensis, E. longicornis, Nephrotoma ferruginea, N. incurva, N. pedunculata, N. tenuis, N. xanthostigma, N. eucera, Tipula angustipennis, T. bella, T. caloptera, T. strepens, T. eluta, T. fraterna, T. cunctans, T. bicornis, T. parshleyi, T. tephrocephala, T. umbrosa.*

3. Species living under bog conditions (oxylophytic), in proximity to Sphagnum — *Limnophila laricicola, Phalacrocera tipulina.*

4. Species inhabiting rocky (lithophytic) situations, usually clinging to the vertical faces of cliffs, hiding in crevices of the rocks, or resting on vegetation growing in such haunts — *Bittacomorphella jonesi, Geranomyia canadensis, G. diversa, Dicranomyia badia, D. stulta, D. simulans, Limnophila montana, Tricyphona auripennis,* Oropeza, *Dolichopeza americana, Tipula macrolabis, T. senega*; the species of Oropeza and Dolichopeza also lurk beneath dark bridges and under culverts.

5. Species inhabiting open gorges, found on the usually luxuriant vegetation of the talus slopes and along the floor of the ravines — *Dicranomyia morioides, D. monticola, Geranomyia diversa, Limnophila cubitalis, Adelphomyia minuta, Ula elegans, Tipula collaris, T. senega, T. taughannock, T. fuliginosa, T. valida.*

6. Species inhabiting shaded, cold Canadian woodlands (mesophytic), usually found on rank vegetation in the shade of hemlock, beech, yellow birch, sugar and red maples, and the like; they occur in close proximity to water, on herbage such as ferns, horsetails, Taxus, Streptopus, Clintonia, Smilacina, Medeola, Laportea, Coptis, Dalibarda, Impatiens, and Viola, from which they may be swept with a net — *Dicranomyia immodesta, D. gladiator, D. halterata, D. pubipennis, D. globithorax, D. macateei, Rhipidia maculata, Limnobia solitaria, L. indigena, L. parietina, L. triocellata, L. tristigma, Elephantomyia westwoodi, Toxorhina mulicbris, Dicranoptycha germana, Atarba picticornis, Ormosia apicalis, O. monticola, Erioptera armillaris, E. megophthalma, E. stigmatica, E. nyctops, Molophilus pubipennis, M. fultonensis, M. hirtipennis, M. comatus, M. ursinus, Gonomyia florens, G. blanda, Cladura delicatula, C. flavoferruginea, Limnophila albipes, L. niveitarsis, L. tenuicornis, L. toxoneura, L. areolata, L. adusta, L. nigripleura, L. subcostata, L. alleni, L. brevifurca, L. aprilina, L. johnsoni, L. fuscovaria, L. rufibasis, L. munda, L. sylvia, L. stanwoodae, L. osborni, L. noveboracensis, L. emmelina, L. edwardi, Adelphomyia americana, A. minuta, A. cayuga, Ulomorpha pilosella, Pedicia albivitta, P. contermina, Tricyphona vernalis, T. katahdin, T. calcar, Rhaphidolabis rubescens, R. tenuipes, R. flaveola, R. modesta, Cylindrotoma americana, C. tarsalis, Liogma nodicornis, Longurio testaceus, Tipula oropezoides, T. algonquin, T. senega, T. hermannia, T. fragilis, T. macrolabis, T. mingwe, T. monticola, T. hirsuta, Trichocera bisinuata, Bittacomorphella jonesi.*

7. Species inhabiting shaded Transitional woodlands (mesophytic), often quite open, in shade of hornbeam, basswood, hickory, butternut, ash, and other trees, usually near running water, occurring on a variety of rank herbage and low vegetation such as Thalictrum, Podophyllum, Menispermum, Nepeta — *Dicranomyia immodesta, D. pudica, D. rostrifera, D. brevivena, D. liberta, D. haeretica, D. morioides, Rhipidia fidelis, Limnobia fallax, L. indigena, L. cinctipes, L. immatura, L. triocellata, Discobola argus, Rhamphidia flavipes, Dicranoptycha sobrina, D. winnemana, Atarba picticornis, Teucholabis complexa, Ormosia nubila, O. innocens, O. nigripila, O. rubella, O. meigenii, Erioptera septemtrionis, E. chrysocoma, E. chlorophylla, E. armata, Molophilus hirtipennis, M. pubipennis, Gonomyia alexanderi, G. sulphurella, G. cognatella, Cladura flavoferruginea, Limnophila macrocera, L. tenuipes, L. adusta, L. subcostata, L. ultima, L. fuscovaria, L. cubitalis, L. quadrata, L. lenta, Epiphragma fascipennis, Adelphomyia americana, Dicranota noveboracensis, D. rivularis, Rhaphidolabis cayuga, R. tenuipes, Nephrotoma ferruginea, N. incurva, N. lugens, N. macrocera, N. tenuis, Tipula unimaculata, T. angustipennis, T. senega, T. apicalis, T. strepens, T. hermannia, T. collaris, T. nobilis, T. grata, T. hebes, T. longiventris, T. morrisoni, T. taughannock, T. fuliginosa, T. submaculata, T. tephrocephala, T. ultima.*

8. Species found in the immediate vicinity of streams and rivers, on the rocks or on trees and bushes near by — *Dicranomyia immodesta, D. badia, D. stulta, D. morioides, D. simulans, Geranomyia diversa, G. canadensis, Antocha saxicola, Cryptolabis paradoxa, Hexatoma megacera, Eriocera brachycera, E. spinosa, E. longicornis, E. cinerea, E. fultonensis, E. tristis, Dicranota noveboracensis, D. rivularis, Tipula bella, T. caloptera, T. eluta, T. strepens.*

9. Species found in southern gum swamps, where the forest cover is largely bald cypress (Taxodium), sweet gum (Liquidambar), sour gums (*Nyssa aquatica* and *N. sylvatica*), and the like, and the herbage consists largely of lizard's-tail (Saururus) — *Gonomyia puer, G. manca, Limnophila recondita, L. luteipennis, L. irrorata, Penthoptera albitarsis, Eriocera wilsonii, Brachypremna dispellens, Tipula tricolor, T. perlongipes, Nephrotoma okefenoke, N. virescens.*

## ACTIVITIES

### *Feeding habits*

The species with elongate rostra (Geranomyia, Toxorhina, Elephantomyia, and others) feed on the nectar of tubular flowers, the Compositae being chosen by most of the species, at least in eastern America. Knab's

(1910) very valuable paper cites in detail the feeding habits of the local species of Geranomyia, which sip the nectar from various composite flowers (Eupatorium, Solidago, Aster, Erigeron, Silphium, Rudbeckia, Verbesina, Cacalia, and others). A few other plant families (Apocynaceae, Ericaceae, Umbelliferae, Rhamnaceae, Lauraceae) are fed upon by various species of crane-flies. The food of the majority of crane-flies, or, indeed, their duration of existence in an adult state, is very little understood. Many species are presumed to be comparatively short-lived and would not require food before the essential functions of reproduction and oviposition were completed; other forms, however, are on the wing for so long a time that it is probable that some sort of food is taken during this period.

*Resting habits*

The Tipulidae vary in their resting habits and in the positions assumed, according to the species and to the habitats frequented. Some (as Molophilus and Erioptera) rest on the vertical or inclined surfaces of trees, cliffs, or buildings, with all the legs far outstretched like those of a spider. Many others habitually rest on the upper or the lower surfaces of leaves. In such positions of rest the wings are usually held outspread, or divaricate, in the Tipulinae, and folded over the abdomen in the Limnobiinae. But such broad generalizations break down even within a single genus. Thus, in Limnophila such species as *munda*, *areolata*, and *niveitarsis* have the wings folded over the back, while *L. toxoneura* and the related *Epiphragma fascipennis* hold the wings divaricate; in the genus *Tipula*, most species of which rest with outspread wings, the species of the *marmorata* group (*fragilis*, *ignobilis*, and others), as well as those of the related genus Longurio, hold the wings incumbent over the abdomen. Some exotic crane-flies (as the genus Thrypticomyia, *Dicranomyia saltens*, and several species of Trentepohlia) habitually rest on spiders' webs. All these species have conspicuously white feet; *Dicranomyia saltens* has a curious horizontal dance along a transverse strand. Species of Dolichopeza and Oropeza living in caves and beneath dark culverts, hang suspended from the roof by one or two pairs of legs. *Limnophila montana*, *Dicranomyia badia*, *D. simulans*, and some other species that live on cliffs, rest flat against the rock with all the legs on the support. Many species of Limnobiini (*Geranomyia canadensis*,

*G. diversa*, *Dicranomyia simulans*, *D. badia*, *D. stulta*) practice a curious up-and-down bobbing while at rest or while feeding, their long, slender legs acting as springs.

*Swarming and mating*

Swarming usually takes place during the early hours of twilight or in the late afternoon. The swarming of the Limnobiinae is a familiar performance. The number of individuals participating varies from two or three to a dozen or twenty in *Rhabdomastix flava*, *Ula elegans*, *Limnophila brevifurca*, *L. ultima*, and *Epiphragma fascipennis*, several hundreds in most species of Ormosia and Erioptera, and vast swarms in species of Trichocera and in *Eriocera longicornis*, in which many thousands of individuals are involved. In practically all cases the start of the swarm is the same. It begins with one or two individuals and is gradually augmented by the arrival of newcomers. Usually the flight is not far above the ground, that of the smaller species (as in the genera Ormosia, Limnophila, Dicranota, and Rhaphidolabis) taking place under the low branches of a tree or the inclined trunk of a fallen log. In Eriocera, however, mating usually takes place in the open, often over the broad expanse of a river or a stream. The vertical height covered by the dance varies from a few inches in some species to many feet in *Brachypremna dispellens*, the "king of the dancing crane-flies." Mating takes place during the swarming, and the united pair generally leaves the main body of the swarm and flies away to a resting place.

The tipuline forms and some of the Limnobiinae (several species of Dicranomyia, species of Hexatoma, *Tipula macrolabis*, *T. fragilis*, *T. fuliginosa*, *T. taughannock*, and others) seem to mate without the preparatory operation of swarming, the males searching diligently and unceasingly for their mates, walking and fluttering about until they encounter the hiding female and then engaging in copulation. As stated by Needham (1908:215) in the case of *Dicranomyia simulans*, the males of this species seem to be very short-sighted and apparently unable to see their mates even when very close to them; they seem to rely mainly on the tactile nature of their long, filiform feet, which, the instant they come in contact with any part of the female, apprise the male of its proximity.

In some groups (Discobola, Liogma, Cylindrotoma, *Tipula ultima*, and others) the males mate with the females while the latter are still callow and teneral, in some cases even waiting beside the pupal case for the female to emerge, when she is at once engaged in copulation. In most cases, however, the female is fully developed and mature before mating takes place. When in copula most species rest quietly on some support, but nearly all species are quite capable of flying while still mated if disturbed; in such cases the larger sex takes the initiative — the female in the Tipulinae, the male in *Eriocera longicornis* and Teucholabis. Cases of mating between different species are rare, but in one instance the writer has noted the copulation of *Phalacrocera tipulina* with *Liogma nodicornis*.

### *Oviposition*

The method of oviposition varies with the species and according to the structure of the ovipositor. In the forms with aquatic larvae (Eriocera, Hexatoma, and others) the eggs are laid directly in the water, the fly dipping during its flight. Many Tipula, such as *T. iroquois*, *T. bella*, and others, deposit their eggs regularly and methodically in algal beds at the edge of a stream. *Tipula nobilis*, one of the species having soft, blunt valves in the ovipositor, lays its eggs in soft mud or in moss. Many species of Limnophila deposit their eggs with great precision. The author has observed females of *Limnophila alleni* flying about low over the earth in cold, dark woods. They flutter along slowly and silently until a suitable place for egg-laying is found, consisting of a moss-covered, rotten log and the mud beneath it. The eggs are pushed firmly into their position by the acicular tergal valves of the ovipositor, considerable effort being made to place them securely. The rate of oviposition is not more than eight or ten eggs a minute, the female often pausing to rest for several seconds during the operation. When engaged in oviposition the fly is quite unconcerned with other agencies and may be picked up by hand.

The species of Tipula with a serrated ovipositor, as described on page 875, undoubtedly have a specialized method of egg-laying, tho what this may be is not yet known.

### *Photophilism*

Many species of crane-flies, in widely separated groups, are attracted to light, such species being termed *photophilous*, or light-loving. It is

probable that this characteristic is fairly general among crane-flies. An interesting fact is that the great majority of specimens of photophilous species taken are either females, or males and females still in copulation, indicating a nocturnal or a crepuscular oviposition or mating habit for these species. There are many of these species, among them being *Erioptera septemtrionis*, *Limnophila adusta*, *Pedicia contermina*, *Nephrotoma ferruginea*, *Tipula apicalis*, *T. trivittata*, and *T. collaris*. It is these photophilous species that are so commonly found in houses, they being for the most part species that came to the lights at some earlier time.

### ENEMIES

At all stages of their existence crane-flies are beset by enemies. The larvae and adults are preyed upon by a great variety of insect-eating birds and amphibia, and by many predacious insects such as beetles, asilid and empidid flies, Odonata, and the like. The larvae are parasitized by certain tachinid flies (Siphona, Admontia), and many internal parasites (Gregarinidae, Bacteria) and fungous diseases (Entomophthora [Empusa]) often prove fatal to crane-flies in their early stages. It is at their periods of transformation and while still soft and teneral that they are most susceptible to attack and injury of all kinds. The adult flies often serve as carriers of little red mites of the genera Trombidium and Rhyncholophus. This condition is very general and a great range of species are affected.

Many species of the family (Geranomyia, Dicranomyia, Limnophila, and others) live on the faces of vertical cliffs which are often wet with percolating and dropping water, and this results in a certain mortality due to the insects' being struck by the falling drops and dashed into the mud. During heavy rainfalls the smaller crane-flies rest on the underside of the leaves of trees, while the larger forms escape injury by hiding in crevices of the rock or the bark or by remaining closely pressed against the trunks of trees.

## KEYS TO THE CRANE-FLIES OF NORTHEASTERN NORTH AMERICA

The species of crane-flies found in northeastern North America are included in four families, which may be separated according to the following key:

1. Five branches of the radius reaching the wing margin; a single anal vein ..... TANYDERIDAE (p. 883)
   Less than five branches of the radius reaching the wing margin; one or two anal veins ..... 2
2. Ocelli present ..... RHYPHIDAE (p. 886)
   Ocelli lacking ..... 3
3. A single anal vein ..... PTYCHOPTERIDAE (p. 884)
   Two anal veins (both running to the wing margin in all North American species; in some Old World forms the first anal vein fused with the second cubitus for a distance backward from the tip) ..... TIPULIDAE (p. 889)

## FAMILY Tanyderidae

The remarkable primitive family Tanyderidae includes but two living genera — Tanyderus, of the antipodal regions, and Protoplasa, of the United States.

### Genus **Protoplasa** Osten Sacken

1859 *Protoplasa* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

There are but two species of Protoplasa. The eastern species, *P. fitchii*, is discussed below. The western species, *P. vipio*, ranges from Colorado to California.

### *Protoplasa fitchii* O. S.

1859 *Protoplasa fitchii* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The species *Protoplasa fitchii* is of medium size and bears a curious superficial resemblance to the common tipulid *Epiphragma fascipennis*. It is a very rare insect, there being scarcely a score of specimens in the various collections, most of them from the Adirondacks of New York State and the Black Mountains of North Carolina. The fly is brownish gray, the wings being marked with an ocellate pattern of spots and bands (Plate XXX, 1). The anal angle of the wing, which is almost square, is very prominent. The immature stages are unknown but the writer surmises that they occur in wet wood in the same situations as the larvae and pupae in the genus Epiphragma.

## FAMILY Ptychopteridae

The family Ptychopteridae has generally been understood to include the tanyderid flies, as well as the three genera herein considered as constituting it. The resemblance between the Tanyderidae and the Ptychopteridae seems to be superficial only, however, and the differences are very considerable.

The immature stages of the Ptychopteridae are very remarkable. The larva lives in an aquatic or a semi-aquatic habitat, and its caudal extremity is provided with an extensile elongated breathing tube which bears the spiracles at the end. The pupa has one of the two thoracic breathing horns enormously elongated, while the other is considerably atrophied. Both these elongated processes in the immature stages serve to provide the insect with air while the body is submerged beneath the mud and water. The larvae of Bittacomorpha are of a peculiar rust-red color; those of Bittacomorphella are almost black, with the short breathing horns yellow; those of Ptychoptera are more yellowish brown.

The following key divides the family into its genera:

1. Antennae 20-segmented; wings with cell $M_2$ lacking; legs banded with black and white. (Subfamily **Bittacomorphinae.**) ..... 2
   Antennae 16-segmented; wings with cell $M_2$ present; legs not banded with black and white. (Subfamily **Ptychopterinae.**) ..... *Ptychoptera* Meig. (p. 884)
2. Apex of the wing not pubescent; metatarsi swollen ..... *Bittacomorpha* Westw. (p. 884)
   Apex of the wing pubescent; metatarsi not swollen ..... *Bittacomorphella* Alex. (p. 885)

### SUBFAMILY Ptychopterinae

#### Genus **Ptychoptera** Meigen

1803 *Ptychoptera* Meig. Illiger's Mag., vol. 2, p. 262.

*Ptychoptera rufocincta* O. S.

1859 *Ptychoptera rufocincta* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

*Ptychoptera rufocincta* is the only eastern species of Ptychoptera. It is deep black, with rusty-red bands on the abdominal segments; the wings (Plate XXX, 2) have brown crossbands, presenting an appearance superficially very like that of *Limnophila macrocera*.

### SUBFAMILY Bittacomorphinae

#### Genus **Bittacomorpha** Westwood

1835 *Bittacomorpha* Westw. London and Edinburgh Phil. Mag., vol. 6, p. 281.

There are two described species of Bittacomorpha inhabiting the Nearctic region, one, *Bittacomorpha clavipes* (Fabr.), in the East, and one, *B. occidentalis* Ald., in the West. *B. clavipes* has been reported from Brazil but the record needs confirmation.

Bittacomorpha, or the "phantom crane-fly," is among the most interesting of the local genera. The larger and commoner eastern species, *B. clavipes*, is one of the most abundant and widely distributed of the North American crane-flies, and inhabits wet swales, swamps, margins of ponds, and similar situations. The legs are curiously banded with black and white. The thoracic dorsum is deep velvety black with a white median line. The swollen metatarsi are unique among the local crane-flies. The wing is shown in Plate XXX, 3. The larva of this species is very similar in structure to that of species of Ptychoptera, but is easily distinguished by the rust-red tomentum which completely covers the body. Both these genera have the extensile breathing tube in the larva, and the single enormously produced breathing spiracle in the pupa. The larvae are common in rotting organic vegetable matter which is percolated and saturated with running water. The adult flies are very conspicuous and attract considerable attention even among persons who are not greatly interested in insects. The long, swollen legs, radiating out from the body like the spokes from the hub of a wheel and conspicuously banded with black and white, make the flies noticeable as they drift slowly thru the air, apparently as light as bits of down.

### Genus **Bittacomorphella** Alexander

1916 *Bittacomorphella* Alex. Proc. Acad. Nat. Sci. Phila., p. 545.

The genus Bittacomorphella includes two known species, both of the Nearctic region. Of these, *Bittacomorphella jonesi* (Johns.) is eastern, and the larger species, *B. sackenii* (Röder), is western. The better-known of the two species, *B. jonesi*, is locally common in cold, shaded situations, as along dark ravines, near running water, or beneath dark bridges and culverts. The curious black larva is found in mud or moist earth, in haunts similar to those described for the adult. The flies are readily distinguished from those of the larger and somewhat similar *Bittacomorpha clavipes* by the metatarsi, which are not swollen and have no white near the base but are marked with more or less white at the tips, these white markings being broadest on the fore legs and narrowest on the hind legs.

The tibiae are black, with a broad white band beyond the base. The second and third tarsal segments are pure white. The apically pubescent wings (Plate XXX, 4) are characteristic of the genus.

## FAMILY Rhyphidae

The family Rhyphidae includes an apparently heterogeneous group of three subfamilies which, until a very recent date, were placed in three widely separated families of the nematocerous Diptera. The Rhyphidae comprise about fifty species, arranged in some seven genera. The family has long been held to contain only the genus Rhyphus and one or two closely allied exotic genera. In 1916, Edwards (1916) removed the genus Mycetobia from the family Mycetophilidae and placed it with the Rhyphidae. A critical study of the immature stages of the genus Trichocera now demonstrates that this group, likewise, should be placed in very close proximity to the Rhyphinae. In general appearance the three groups or subfamilies herein considered as comprising the Rhyphidae differ greatly, but the larvae of all members are so unmistakably related that there can be no question of the close phylogenetic relationship.

The Trichocerinae have the more generalized wing venation, there being three branches to the sector and three to the media, and two distinct anal veins. The local species of Trichocera have the *m-cu* cross-vein punctiform or obliterated by a slight fusion of $Cu_1$ on $M_3$. *Trichocera trichoptera* O. S., of the Western States, has the cross-vein very long and conspicuous. The second anal vein is long and subsinuate in the subgenus Diazosma Bergr., but very short and recurved in the typical subgenus, in *T. trichoptera* being very short and reduced and narrowing the second anal cell.

Edwards (1916) and Knab (1916) have recently shown the probable evolution of Mycetobia from the more generalized Rhyphidae such as Rhyphus and Olbiogaster. The most important venational feature to be considered is the reduction of the media in the Mycetobiinae, but two branches persisting in Mycetobia and the vein tending to be evanescent in the Ethiopian genus Mesochria. Species of Olbiogaster in some cases have the posterior branch of the media less strongly chitinized than the anterior fork, and probably indicate the manner in which the vein is reduced. An entirely comparable case is seen in the related family Ptychopteridae (comparing Ptychoptera and Bittacomorpha). In the

Rhyphidae, the Trichocerinae are the most generalized, the Mycetobiinae the most specialized, of the groups.

The subfamilies may be separated by the following key:

1. Two distinct anal veins; radial sector three-branched..... **Trichocerinae** (p. 887)
   A single distinct anal vein; radial sector two-branched.....2
2. Cell *1st* $M_2$ present..... **Rhyphinae** (p. 888)
   Cell *1st* $M_2$ lacking..... **Mycetobiinae** (p. 888)

## SUBFAMILY Trichocerinae

The subfamily Trichocerinae includes but two genera — Trichocera, and Ischnothrix Bigot of Cape Horn.

### Genus **Trichocera** Meigen

1800 *Petaurista* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Trichocera* Meig. Illiger's Mag., vol. 2, p. 262.
1911 *Paracladura* Brun. Rec. Indian Mus., vol. 6, p. 286.

In the genus Trichocera there are about twenty described species, of which the majority are Holarctic in their distribution but a few are from India and the antipodes. The species of this genus are in a very chaotic condition taxonomically, and it seems difficult to remedy this until the European and American forms can be critically studied and compared. There can be little doubt that many of the species are Holarctic in their distribution and the three or four evident species within the limits here considered may be conspecific with the European forms. The larvae, so far as known, live in decaying vegetable matter (Johannsen, 1910). The adult flies are common in autumn and early spring, and appear in small swarms on warm, sunny days in winter. During the winter months they are often found in cellars, resting on the windows. They are also to be found in mines, and the writer has seen specimens from a Colorado silver mine taken at a very considerable depth by Dr. H. B. Hungerford. Some of the swarms of these flies number many thousands of individuals.

The following key divides the local species of Trichocera:

1. Second anal vein subsinuate; veins long-hairy; ovipositor fleshy. (Subgenus *Diazosma* Bergr.) [Journ. N. Y. Ent. Soc., vol. 24, p. 124–125, pl. 8, fig. 10. 1916.] (Plate XLI, 166.)..... *T. subsinuata* Alex.
   Second anal vein short, incurved to the anal angle; veins not long-hairy; ovipositor chitinized, turned downward, the concavity being on the lower face. (Subgenus *Trichocera* Meig.)..... 2
2. Wings with two brown clouds. [List Dipt. Brit. Mus., vol. 1, p. 84. 1848.]
   *T. bimacula* Walk.
   Wings unicolorous. [Winter Insects of New York, p. 9. 1848.] (Plate XLI, 165.)
   *T. brumalis* Fitch

Certain European species of Trichocera, such as *T. maculipennis* (Fabr.) and *T. regelationis* (Linn.), have been recorded from the Northern States and Canada; these records may be correct, since, as stated above, it is very probable that many species of the genus are Holarctic in their distribution. If such is the case, the names used in the preceding key are very probably synonyms of the European species.

## SUBFAMILY Rhyphinae

The subfamily Rhyphinae includes but three genera. The two which are represented by North American species are Rhyphus, with about a score of principally Holarctic species, and Olbiogaster, a tropical group of five species. Within the limits of this paper three species occur, two of which — *Rhyphus fenestralis* and *R. punctatus* — are very widespread over the North Temperate Zone.

### Genus **Rhyphus** Latreille

1805 *Rhyphus* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 291.

The adult flies of the genus Rhyphus are often found resting on the trunks of trees or on near-by vegetation. The immature stages are spent in decaying vegetable matter, manure, sewage, and similar situations. The venation of a typical Rhyphus is shown in figure 132, A.

Baerg (1918) has recently published a key for the separation of the adult flies of the three eastern-North-American species of the genus. This key is here modified to conform with the other keys in this paper:

1. Basal deflection of $M_2$ as long as, or longer than, $m$ (that is, veins $M_1$, $M_2$, and $M_3$ about equidistant from one another at cell *1st* $M_2$) ..... 2
   Basal deflection of $M_2$ much shorter than $m$; eyes of male holoptic; no yellowish spot near midlength of costal margin of wing ..... *R. punctatus* (Fabr.)
2. Wing with a distinct yellowish spot near midlength of costal margin; subapical hyaline spots sharply defined; eyes of male holoptic; median prescutal stripe split by a narrow gray line, more distinct in the female ..... *R. alternatus* Say
   Wing with the yellow and hyaline spots less distinct and more diffuse; eyes of both sexes dichoptic; median prescutal stripe only indistinctly divided, if at all. *R. fenestralis* (Scop.)

## SUBFAMILY Mycetobiinae

The subfamily Mycetobiinae, so far as known, includes only the genus Mycetobia, discussed below, and the genus Mesochria of the Seychelles Islands. Other genera have been associated with Mycetobia in the Mycetophilidae, but so far as is known their larvae are quite normal for

the latter family and quite unlike the amphipneustic larvae of the Rhyphidae. Until additional data are forthcoming they should be considered as being Mycetophilidae.

### Genus **Mycetobia** Meigen

1818 *Mycetobia* Meig. Syst. Beschr., vol. 1, p. 229.

Johannsen (1909) recognizes six recent species of Mycetobia, and five others as fossil in Baltic amber (Eocene). The larvae are found in decaying

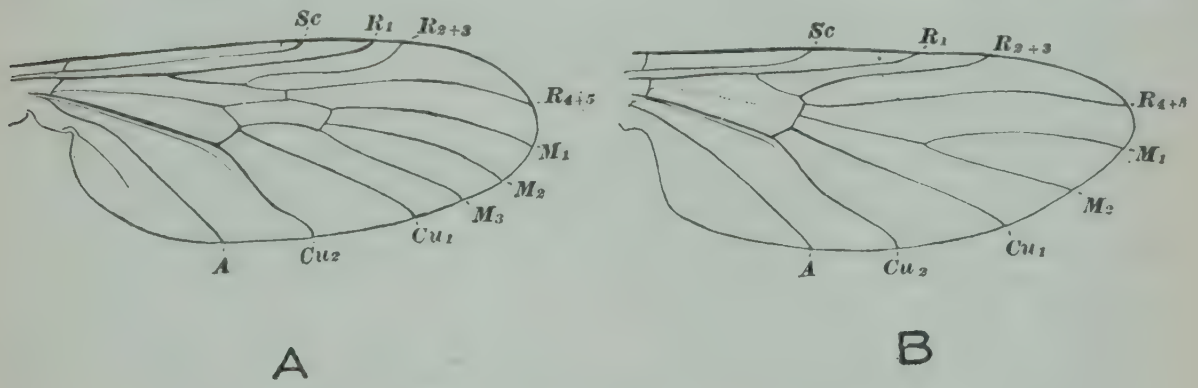


FIG. 132. WING VENATION IN RHYPHIDAE

A, Venation of typical Rhyphus. B, Venation of Mycetobia

trees and in fermented sap in the wounds of trees. A single species is known from New York State, *Mycetobia divergens* Walk. The characteristic venation of the genus is shown in figure 132, B.

## FAMILY **Tipulidae**

The family Tipulidae includes almost all of the local crane-flies. It is divided into three subfamilies, two of which are further separable into nine tribes — six belonging to the Limnobiinae and three to the Tipulinae. The tribes may be separated as follows:

1. Last segment of the palpi elongate, whiplash-like; nasus usually distinct; antennae usually with 13 segments; *Sc* almost always ending in *R*; *m-cu* cross-vein present or obliterated by the usually slight fusion of $Cu_1$ on $M_{3+4}$. In the dolichopezine genus Brachypremna (p. 928) *Sc* is very long and ends in the costa, and the fusion of $Cu_1$ and $M_{3+4}$ is often extensive; but the antennae are 13-segmented, the palpi are elongated, the nasus is distinct, and the whole appearance of the fly is decidedly tipuline. (Subfamily **Tipulinae**.) . . . . . 2

   Last segment of the palpi short; no distinct nasus; antennae usually 14- or 16-segmented; *Sc* usually ending in costa but connected with *R* by $Sc_2$; *m-cu* cross-vein obliterated by the long fusion of $Cu_1$ on $M_{3+4}$. In Pedicia (p. 923) the palpi are elongated, but all other characters are limnobiine. (Subfamilies **Limnobiinae, Cylindrotominae**.) . . . . 4

2. Vein $R_2$ obliterated by atrophy (this is also the case to a lesser extent in *Tipula subfasciata* and *T. penobscot*), or else (as in Brachypremna) the second anal vein very short, not more than one-third the length of the first anal vein; legs very slender, filiform ..... *Dolichopezini* (p. 928)
   Vein $R_2$ present for its entire length (except in *Tipula subfasciata*, *T. penobscot*, and other species); second anal vein longer, one-half the length of first anal vein; legs stouter and usually shorter than in Dolichopezini ..... 3
3. Antennae without verticils (see Stygeropis, below); flagella of the male antennae pectinate ..... *Ctenophorini* (p. 930)
   Antennae verticillate (except in Stygeropis and most species of Holorusia); flagella of the male antennae not pectinate (in some species of Nephrotoma and Tipula the ventral face of the segments is often deeply incised, producing a serrate appearance, but the antennae in the northern forms are never pectinate) ..... *Tipulini* (p. 932)
4. Four branches of radius reaching the margin (see note on *Gonomyia blanda*, below) ..... 5
   Two or three branches of radius reaching the margin ..... 9
5. Tibiae spurred at tip ..... 6
   Tibiae without spurs at tip. (*Gonomyia blanda*, p. 905, has $R_2$ in close proximity to $R_1$ at the wing margin, so that but three branches of the radius appear to reach the wing margin; the tropical antochine genus Paratropeza will also run to here, and has been mistaken by some authors for a Gnophomyia; the investigator must always be on the lookout for such aberrant genera and species, especially when dealing with tropical material.) ..... *Eriopterini* (p. 901)
6. Antennae with from 6 to 10 segments ..... *Hexatomini* (p. 920)
   Antennae with more than 10 segments ..... 7
7. $Sc_2$ beyond the origin of $Rs$ ..... *Limnophilini* (p. 913) (except genus Ula)
   $Sc_2$ before the origin of $Rs$ ..... 8
8. Antennae 17-segmented; wings pubescent ..... Genus *Ula*, tribe *Limnophilini* (p. 913)
   Antennae 13- to 16-segmented; wings glabrous ..... *Pediciini* (p. 923)
9. Tibiae spurred; an apparent fusion of $R_{1+2+3}$ to the wing margin so that but two branches of the radius are present (except in *Phalacrocera neoxena*, in which three branches are present). The European hexatomine genus Cladolipes runs to here but has only eight antennal segments; the South American species *Psaronius abnormis* also comes here, but may be readily separated by the very elongate subcosta.
   Subfamily **Cylindrotominae** (p. 926)
   Tibiae without spurs; no contiguity of $R_1$ and $R_{2+3}$ at their tips ..... 10
10. Antennae 12-, 15-, or 16-segmented; claws usually without teeth on their lower side ..... 11
    Antennae 14-segmented; claws with teeth on their lower side ..... *Limnobiini* (p. 890)
11. Cross-vein *r* lacking; *Sc* ending before the origin of the short *Rs*; $R_{2+3}$ upcurved at the end, $R_{4+5}$ bent strongly toward the apex of the wing producing a trumpet-shaped cell $R_3$; cell *1st* $M_2$, when present, pointed at the inner end.
    Subgenus *Leiponeura*, genus *Gonomyia*, tribe *Eriopterini* (p. 905)
    Cross-vein *r* present or lacking; if lacking, *Sc* ends far beyond the origin of *Rs*; $R_{2+3}$ not strongly upcurved at end, and $R_{4+5}$ not bent strongly toward the apex of the wing; inner end of cell *1st* $M_2$ not pointed ..... *Antochini* (p. 897)

The nearly wingless snow fly, Chionea, belongs to the tribe Eriopterini (page 902).

## SUBFAMILY **Limnobiinae**

### Tribe **Limnobiini**

The genera of the tribe Limnobiini may be separated by the following key:

1. Rostrum elongated, longer than head and thorax together ..... *Geranomyia* Hal. (p. 891)
   Rostrum not elongated, shorter than the head ..... 2

2. A supernumerary cross-vein in cell *1st A*, connecting the two anal veins.
*Discobola* O. S. (p. 892)
No supernumerary cross-vein in cell *1st A* ..... 3
3. Often with a supernumerary cross-vein in cell *Sc*; antennae of the male bi-, uni-, or sub-pectinated ..... *Rhipidia* Meig. (p. 892)
No supernumerary cross-vein in cell *Sc* (excepting a weak one in *Dicranomyia simulans*); antennae of the male not pectinated ..... 4
4. *Sc* usually short, ending opposite the origin of *Rs*; claws usually with but a single tooth on the lower side; ventral pleural appendage of the male hypopygium a fleshy lobe.
*Dicranomyia* Steph. (p. 893)
*Sc* always elongate, ending far beyond the origin of *Rs*; *r* often considerably removed from the tip of $R_1$; claws usually with two or three teeth on the lower side; ventral pleural appendage of the male hypopygium horny ..... *Limnobia* Meig. (p. 895)

## Genus **Geranomyia** Haliday

1833 *Geranomyia* Hal. Ent. Mag., vol. 1, p. 154.
1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683.
1838 *Aporosa* Macq. Dipt. Exot., vol. 1, p. 62.
1865 *Plettusa* Phil. Verh. Zool.-Bot. Ges. Wien, p. 597.

The genus Geranomyia includes about seventy described forms, the species being most numerous in the Neotropical and Oriental regions. The species are readily distinguished from all other crane-flies by the curious elongate rostrum (fig. 124, A, page 846). The four species occurring within the limits considered in this paper are common and widely distributed; further notes on their distribution have been given by the writer in an earlier paper on the genus (Alexander, 1916:486–496). Nothing is known concerning their immature stages, this being one of the most conspicuous gaps in the whole family. It is probable that *G. rostrata*, at least, is partly aquatic, living in moist earth or possibly in wet moss.

The following key divides the local species of the genus:

1. Wings heavily spotted with dark brown; tips of the tibiae black. [*Limnobia rostrata* Say. Journ. Acad. Nat. Sci. Phil., vol. 3, p. 22. 1823.] (Plate XXXI, 10.) ..... *G. rostrata* (Say)
Wings unmarked or with only pale indistinct seams along the cord ..... 2
2. *Sc* short, ending opposite or just beyond the origin of *Rs*; cross-veins and deflections of veins faintly seamed with darker. [Proc. Acad. Nat. Sci. Phil., p. 207. 1859.] (Plate XXXI, 13.) ..... *G. diversa* O. S.
*Sc* long, ending at about midlength of the sector; wings unmarked except for the stigmal spot ..... 3
3. Body coloration yellow; wings with the stigma pale; legs dull yellow, the femora not darkened at their tips. [Journ. N. Y. Ent. Soc., vol. 8, p. 186, pl. 7, fig. 13. 1900.] (Plate XXXI, 12.) ..... *G. distincta* Doane
Body coloration yellowish brown, darkest on the scutal lobes and the postnotum; wings with the stigma oval, dark brown, well-defined; legs brownish yellow, the femora brown at the tips. [*Limnobiorhynchus canadensis* Westw. Ann. Soc. Ent. France, vol. 4, p. 684. 1835.] (Plate XXXI, 11.) ..... *G. canadensis* (Westw.)

*G. canadensis* is most commonly found along small streams near cliffs; *G. diversa*, resting on vegetation along running water or clinging to vertical wet banks; *G. rostrata*, on rich vegetation in damp places, where it is often extremely abundant (Alexander, 1912:67–68). The habits of the adult flies are discussed on page 878.

### Genus **Discobola** Osten Sacken

1865 *Discobola* O. S. Proc. Ent. Soc. Phila., p. 226.
1869 *Trochobola* O. S. Mon. Dipt. N. Amer., part 4, p. 98.

The genus Discobola is a well-defined group including eight described species with a curious discontinuous distribution — two species occurring in North America, two in Europe, and four in New Zealand. The species are readily distinguished by the presence of a strong supernumerary cross-vein between the two anal veins. The only local species is *D. argus*.

### *Discobola argus* (Say)

1824 *Limnobia argus* Say. Long's Exped., App., p. 358.
1865 *Discobola argus* O. S. Proc. Ent. Soc. Phila., p. 226.

The species *Discobola argus* is a curious fly, with ocellate markings on the yellowish white wings (Plate XXXII, 41). The body coloration is yellowish, the thorax with three brown stripes, each femur with a brown subterminal ring. The immature stages of the American species are unknown but are probably spent in decaying pine stumps, as are those of the European *D. caesarea*; specimens of *D. argus* have been observed mating on the bark of stumps (in Ithaca, New York, October 3, 1912, by Ilg and Alexander). The fly is uncommon in May and June but becomes more numerous from August to October.

### Genus **Rhipidia** Meigen

1818 *Rhipidia* Meig. Syst. Beschr., vol. 1, p. 153.

In the genus Rhipidia there are about twenty-eight described species, most numerous in the tropics of the New World. The character of the pectination of the antennae (page 851) varies in the different groups or subgenera as follows:

*Rhipidia* Meig. (*maculata*, *bryanti*) — antennae of the male bipectinate.
*Monorhipidia* Alex. (*fidelis*) — antennae of the male unipectinate.
*Arhipidia* Alex. (*domestica*, *shannoni*) — antennae of both sexes subpectinate to simple.

The immature stages of the known species are spent in decaying vegetable matter, manure, or decaying fungi (*R. maculata*, *R. domestica*), in decaying wood or beneath the loose bark of trees (*R. uniseriata*, *R. fidelis*, *R. bryanti*), or perhaps in aquatic situations (*R. maculata*, according to Needham).

The following key divides the local species of the genus:

1. Wings with an abundant pale brown or gray dotting in all the cells.....2
   Wings with the markings larger and confined to the vicinity of the veins.....3
2. Body coloration grayish, the prescutum with a broad black median line; postnotum gray; wings with a heavy brown pattern along the costal margin, the marks about equal to the interspaces; legs brown; male antennae bipectinate. [Syst. Beschr., vol. 1, p. 153, pl. 5, fig. 11. 1818.] (Plate XXXII, 36.).....*R. maculata* Meig.
   Body coloration yellowish brown, the prescutum without a broad black median line; postnotum black; wings with small black spots at the base, the subcostal cross-vein, the origin of the sector, and the stigma, these marks much smaller than the interspaces; legs yellow; male antennae subpectinate. [Proc. Acad. Nat. Sci. Phila., p. 581, pl. 27, fig. 23. 1914.] (Plate XXXII, 39.).....*R. shannoni* Alex.
3. Prescutum reddish brown with narrow black lines; pleura dull yellow with two narrow blackish longitudinal stripes; antennae with segments 12 and 13 light yellowish; basal deflection of $Cu_1$ usually far before the fork of $M$; antennae of the male subpectinate. [Proc. Acad. Nat. Sci. Phila., p. 208, pl. 3, figs. 8, 9. 1859.] (Plate XXXII, 40.)
   *R. domestica* O. S.
   Prescutum gray with a broad black median line; pleura grayish or plumbeous, unstriped; antennae black thruout; basal deflection of $Cu_1$ at the fork of $M$; antennae of the male not subpectinate.....4
4. Wings with the dark pattern beyond the origin of the sector only, a large rounded cloud at the origin and fork of the sector, the large rectangular stigma and the radial cells largely darkened; abdomen dark brown, the genitalia reddish yellow; antennae of the male unipectinate. [Proc. Acad. Nat. Sci. Phila., p. 209. 1859.] (Plate XXXII, 38.).....*R. fidelis* O. S.
   Wings with a series of about five large grayish brown blotches along the costal margin, two before the origin of the sector; abdominal tergites yellow, the caudal half of each segment dark brown; antennae of the male bipectinate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 123, 124, pl. 16, fig. 20. 1909.] (Plate XXXII, 37.).....*R. bryanti* Johns.

*R. domestica* and *R. shannoni* are more southern in their distribution, *R. fidelis* and *R. maculata* more northern. Some of the species have a very extensive geographical range, *R. domestica* and its races occurring from Alaska to Argentina, and *R. maculata* being found thruout northern Europe and North America.

## Genus **Dicranomyia** Stephens

1829 *Dicranomyia* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Siagona* Meig. Syst. Beschr., vol. 6, plate 65, fig. 7.
1854 *Numantia* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 2, p. 470.

Dicranomyia is one of the largest of the crane-fly genera, there being from one hundred and eighty to one hundred and ninety described species

found on all the continents and on many of the oceanic islands. The species are rather small, are dull-colored, and are often difficult of exact determination.

The immature stages are spent in a wide range of habitats, described on page 838

The local species of the genus Dicranomyia may be separated according to the following key:

1. Wings with but one free branch of the media reaching the margin. [23d Rept. N. Y. State Ent., p. 211–212, pl. 27, fig. 5. 1908.] (Plate XXXI, 15.) . . *D. whartoni* Needm.
   Wings with two free branches of the media reaching the margin . . . . . 2
2. Wings narrow, lanceolate; cell *1st* $M_2$ open; thoracic pleura with a brown longitudinal stripe. [*Limnobia longipennis* Schum. Beitr. zur Ent., vol. 1, p. 104, pl. 1, fig. 2. 1829.] (Plate XXXI, 14.) . . . . . *D. longipennis* (Schum.)
   Wings broad . . . . . 3
3. *Sc* ending opposite, or before or slightly beyond the origin of the sector . . . . . 4
   *Sc* ending far beyond the origin of the sector . . . . . 20
4. Antennae with at least the basal segments pale . . . . . 5
   Antennae with the segments dark thruout . . . . . 9
5. Cell *1st* $M_2$ open (cross-vein *m* lacking) . . . . . 6
   Cell *1st* $M_2$ closed . . . . . 7
6. Prescutum with a single brown stripe; dorsal pleural appendage of the male hypopygium a short hook. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] . . . . . *D. immodesta* O. S.
   Prescutum with three brown stripes; dorsal pleural appendage of the male hypopygium a long, saber-like hook, which is contiguous with its mate on the opposite side. [Proc. Acad. Nat. Sci. Phila., p. 212, pl. 3, fig. 5. 1859.] . . . . . *D. gladiator* O. S.
7. Pale yellowish thruout, only the tips of the tarsi and the eyes darker; in life the abdominal segments somewhat greenish. [Proc. Acad. Nat. Sci. Phila., p. 212. 1859.] (Plate XXXI, 22.) . . . . . *D. pudica* O. S.
   Brownish yellow, the antennae darkened at the tips; halteres brownish . . . . . 8
8. Halteres pale, the knobs infuscated; abdomen brownish yellow. [Journ. N. Y. Ent. Soc., vol. 8, p. 183, pl. 7, fig. 5. 1900.] . . . . . *D. isabellina* Doane
   Halteres and abdomen brown. [Proc. Acad. Nat. Sci. Phila., p. 212. 1859.] *D. diversa* O. S.
9. Cell *1st* $M_2$ open; *Sc* far before the origin of *Rs*, due to the shortness of the latter which is about equal to the basal deflection of $R_{4+5}$ . . . . . 10
   Cell *1st* $M_2$ closed; *Sc* nearly opposite the origin of *Rs*, which is much longer than the basal deflection of $R_{4+5}$ . . . . . 11
10. Rostrum elongated, nearly as long as the head, brown; prescutum with a single dark brown stripe. [Mon. Dipt. N. Amer., part 4, p. 65. 1869.] (Plate XXXI, 16.) *D. rostrifera* O. S.
    Rostrum much shorter than the head, light yellow; prescutum with three dark brown stripes. [Mon. Dipt. N. Amer., part 4, p. 66. 1869.] . . . . . *D. brevivena* O. S.
11. Thorax shining black, the pleura with a grayish pruinosity. [Proc. Acad. Nat. Sci. Phila., p. 17. 1860.] (Plate XXXI, 23.) . . . . . *D. morioides* O. S.
    Thorax not shining black; gray, brown, or yellowish brown . . . . . 12
12. Femora brown with the tips broadly yellow; wings marked with brown. [*Limnobia badia* Walker. List Dipt. Brit. Mus., vol. 1, p. 46. 1848.] (Plate XXXI, 20.) *D. badia* (Walk.)
    Femora not banded with yellow; wings unmarked or nearly so . . . . . 13
13. $Sc_1$ much longer than $Sc_2$, being nearly if not quite the length of the stigma . . . . . 14
    $Sc_1$ short, not more than one-half the length of the stigma . . . . . 16

14. Halteres elongated (northern species). [Mon. Dipt. N. Amer., part 4, p. 71. 1869.] (Plate XXXI, 18.) ..... *D. halterata* O. S.
Halteres short, of normal length ..... 15
15. Prescutum reddish brown, with a narrow paler median line. [Journ. N. Y. Ent. Soc., vol. 8, p. 184, pl. 7, fig. 6. 1900.] ..... *D. brunnea* Doane
Prescutum dark brown with yellow and brown stripes. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] ..... *D. distans* O. S.
16. Coloration gray, the prescutum with a broad median brown stripe; a narrow brown seam on cross-vein *r*. [Proc. Acad. Nat. Sci. Phila., p. 209, pl. 3, figs. 4, 4a. 1859.] (Plate XXXI, 21.) ..... *D. liberta* O. S.
Coloration brown or yellowish brown; no narrow brown seam on cross-vein *r* ..... 17
17. Basal deflection of $M_{1+2}$, forming the inner end of cell *1st* $M_2$, arcuated so that cells *1st* $M_2$ and $R_3$ are almost on a line. [Proc. Acad. Nat. Sci. Phila., p. 210. 1859.] ..... *D. stulta* O. S.
Basal deflection of $M_{1+2}$ not conspicuously arcuated, cell *1st* $M_2$ being conspicuously more distant from the wing base than cell $R_3$ ..... 18
18. Thorax brown, with three blackish stripes on the prescutum which are confluent, the lateral ones running caudad onto the scutal lobes; wings hyaline, unmarked. [*Furcomyia monticola* Alex. Psyche, vol. 18, p. 201–202, pl. 16, fig. 7. 1911.] (Plate XXXI, 19.) ..... *D. monticola* (Alex.)
(*Dicranomyia monticola* may not be distinct from *D. stulta*, which appears to be a somewhat variable species.)
Thorax not so marked; wings with a grayish or brownish tinge ..... 19
19. Thorax brownish yellow, with a darker brown median stripe; antennae black. [Mon. Dipt. N. Amer., part 4, p. 70–71, pl. 1, fig. 3. 1869.] (Plate XXXI, 17.) *D. haeretica* O. S.
Thorax light brown without a distinct darker median stripe; antennae reddish brown. [Journ. N. Y. Ent. Soc., vol. 8, p. 184, pl. 7, fig. 8. 1900.] .... *D. moniliformis* Doane
20. Wings spotted with darker ..... 21
Wings unmarked, except for the stigmal spot when it occurs ..... 22
21. Wings with brown dots in all the cells; femora with a yellowish ring before the tip. [*Limnobia simulans* Walk. List Dipt. Brit. Mus., vol. 1, p. 45. 1848.] (Plate XXXI, 24.) ..... *D. simulans* (Walk.)
Wings with three large brown spots along the costa, the first at the origin of the sector, the second at the tip of *Sc*, and the third at the tip of $R_1$; wings grayish brown, paler near the stigma; cord and outer end of cell *1st* $M_2$ seamed with dark brown; femora without a yellowish ring before the tip. [Mon. Dipt. N. Amer., part 4, p. 75. 1869.] (Plate XXXI, 25.) ..... *D. rara* O. S.
22. Wings with a distinct pubescence in the apical cells. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] (Plate XXXI, 28.) ..... *D. pubipennis* O. S.
Wings glabrous on all the cells ..... 23
23. No stigmal spot nor brown seams to the veins; $R_1$ strongly curved toward $R_{2+3}$ at the tip; tarsi brown. [Mon. Dipt. N. Amer., part 4, p. 74. 1869.] (Plate XXXI, 27.) *D. globithorax* O. S.
Stigma evident, dark brown; paler brown seams to the cord and the outer end of cell *1st* $M_2$; $R_1$ not incurved toward $R_{2+3}$; tarsi whitish. [Can. Ent., vol. 48, p. 42–43. 1916.] (Plate XXXI, 26.) ..... *D. macateei* Alex.

## Genus **Limnobia** Meigen

1800 *Amphinome* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Limonia* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Limnobia* Meig. Syst. Beschr., vol. 1, p. 116.
1856 *Limnomyza* Rond. Prodromus, vol. 1, p. 185.

Limnobia is a rather small genus of usually handsome flies, including about thirty-five described species. The species are most numerous in Europe and North America, but a very few range into the tropics of both hemispheres. Most of the crane-flies described as species of Limnobia before the partition of the genus, do not belong here at all.

The haunts of the immature stages, so far as known, include a considerable range of habitats, from possibly aquatic forms (*L. parietina*) to those living in moist earth near streams (*L. fallax* and probably *L. solitaria*), in decaying vegetable matter (*L. indigena*, according to Greene), in decaying leaves (*L. nigropunctata*, *L. flavipes*, *L. tripunctata*), in rotten wood (*L. cinctipes*, *L. annulus*, *L. dumetorum*, and others), and in fungi (*L. triocellata*, *L. xanthoptera*, and often *L. cinctipes* and *L. annulus*).

The local species of Limnobia may be separated according to the following key:

1. Cross-vein *r* at the tip of $R_1$ ..... 2
   Cross-vein *r* removed from the tip of $R_1$ ..... 7
2. Knob of the halteres black ..... 3
   Knob of the halteres pale at the apex ..... 6
3. Femora yellow, the extreme tips narrowly dark brown; wings yellowish, with three eye-like markings. [Proc. Acad. Nat. Sci. Phila., p. 216. 1859.] (Plate XXXII, 34.) ..... *L. triocellata* O. S.
   Femora with one or more dark brown rings before the dark tips; wings without an ocellate pattern ..... 4
4. Wings with four large dark brown spots in cell *R* that are about equidistantly spaced. [Proc. Acad. Nat. Sci. Phila., p. 289. 1861.] ..... *L. hudsonica* O. S.
   Wings not with four large brown equidistant spots in cell *R* ..... 5
5. Small, wing of female about 9.5 mm.; wings narrow, with a distinct dark brown pattern; spots in cell *R* small, clear-cut, dark brown. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 125. 1909.] (Plate XXXII, 32.) ..... *L. fallax* Johns.
   Larger, wing of female about 11 mm.; wings broader, with the pattern paler brown, more diffused; spots in cell *R* larger, often poorly defined and sometimes confluent, medium brown. [Proc. Acad. Nat. Sci. Phila., p. 215, pl. 3, fig. 6. 1859.] (Plate XXXII, 31.) ..... *L. solitaria* O. S.
6. Femora with three brown bands. [Proc. Acad. Nat. Sci. Phila., p. 214. 1859.] ..... *L. immatura* O. S.
   Femora with two brown bands. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21. 1823.] (Plate XXXII, 29.) ..... *L. cinctipes* Say
7. Wings with brown clouds and seams ..... 8
   Wings nearly clear, at most with three or four small brown dots along the costal margin ..... 9
8. Large species, wing 15 mm.; wing apex very blunt; all the cells clouded and marbled medially with gray and brown. [Proc. Acad. Nat. Sci. Phila., p. 289. 1861.] (Plate XXXII, 30.) ..... *L. parietina* O. S.
   Small species, wing under 12 mm.; wing apex normal; apical cell with the markings confined to the region near the veins. [Proc. Acad. Nat. Sci. Phila., p. 215, pl. 3, fig. 3. 1859.] (Plate XXXII, 33.) ..... *L. indigena* O. S.

9. Wings with three small brown dots along the costal margin; head dark; antennae darkened toward the tips. [Proc. Acad. Nat. Sci. Phila., p. 216. 1859.] (Plate XXXII, 35.) *L. tristigma* O. S.
Wings yellowish, unspotted; head yellow, excepting the front; antennae yellow. [Mon. Dipt. N. Amer., part 4, p. 95. 1869.] ..... *L. sociabilis* O. S.

*Limnobia cinctipes* runs very close to *L. immatura* and apparently cannot always be distinguished from it; the character of an ocellate, yellow, brown-encircled mark at the stigma in *L. cinctipes* and a solid brown one in *L. immatura* does not hold in a series. *L. hudsonica*, *L. solitaria*, and *L. fallax* represent another group of closely related species. *L. sociabilis* is very rare and its exact status is still not well understood.

## Tribe **Antochini**

The genera of the tribe Antochini may be classified in accordance with the following key:

1. Rostrum elongated, at least as long as the head ..... 2
Rostrum shorter than the head ..... 4
2. Rostrum about as long as the head or a very little longer ..... *Rhamphidia* Meig. (p. 897)
Rostrum about as long as the body ..... 3
3. *Rs* with two branches reaching the wing margin ..... *Elephantomyia* O. S. (p. 898)
*Rs* with a single branch reaching the wing margin ..... *Toxorhina* Loew (p. 898)
4. Cross-vein *r* lacking ..... *Atarba* O. S. (p. 899)
Cross-vein *r* present ..... 5
5. Anal angle of the wing prominent, almost square; *Rs* very elongate, straight; basal deflection of $Cu_1$ before the fork of *M* ..... *Antocha* O. S. (p. 899)
Anal angle of the wing feeble; *Rs* shorter, more arcuated; basal deflection of $Cu_1$ at or beyond the fork of *M* ..... 6
6. $R_1$ beyond the tip of *Sc* long, longer than the sector alone; veins issuing from cell *1st* $M_2$ very long ..... *Dicranoptycha* O. S. (p. 900)
$R_1$ beyond the tip of *Sc* short, less than the length of the sector alone; veins issuing from cell *1st* $M_2$ short ..... *Teucholabis* O. S. (p. 901)

The author's key to the Antochini given in Psyche (volume 20, pages 40–41, 1913) is erroneous in the disposition of Dicranoptycha, which runs down into the couplet with Atarba as having the radial cross-vein lacking. The key was based on material that was not normal and should be emended as above.

### Genus **Rhamphidia** Meigen

1830 *Rhamphidia* Meig. Syst. Beschr., vol. 6, p. 281.

About eighteen species of the genus Rhamphidia are known, and they are distributed thruout all the major regions of the world. The larva of *Rhamphidia longirostris* (Palaearctic) has been found in the stems of

*Rumex aquaticus*. The two local species live in organic mud in swamps, and both the larvae and the pupae are decidedly eriopterine in appearance.

The local species of the genus Rhamphidia may be separated in accordance with the following key:

Rostrum short; legs yellow, tips of femora and tibiae black; wings tipped with dusky. [Dipt. Exot., 5th supp., p. 17. 1855. Osten Sacken, Mon. Dipt. N. Amer., part 4, p. 105–106. 1869.] (Plate XXXIII, 42.) ..... *R. flavipes* Macq.

Rostrum long; legs uniformly dark brown; wings uniformly subhyaline, not tipped with dusky. [Proc. Acad. Nat. Sci. Phila., p. 498–499, pl. 25, fig. 14. 1916.] (Plate XXXIII, 43.) ..... *R. mainensis* Alex.

## Genus **Elephantomyia** Osten Sacken

1859 *Elephantomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

The genus Elephantomyia includes about eight species, found in North America, Europe, Africa, and eastern Asia. The complete wing venation separates the flies from all other genera with an elongate rostrum, except the Oriental genus Rhampholimnobia Alex. The immature stages of the known species are spent in decaying wood.

### *Elephantomyia westwoodi* O. S.

1869 *Elephantomyia westwoodi* O. S. Mon. Dipt. N. Amer., part 4, p. 109, pl. 1, fig. 5.

The species *Elephantomyia westwoodi* is a curious fly inhabiting cold Canadian woods and bogs, where it is found on the wing from late June into August. R. C. Shannon collected larvae at Washington in late November of 1912, and again on May 2, 1913, and reared the fly. It had been bred before by Johnson.

The adult is yellow with the abdominal segments ringed caudally with brown and the wings having a distinct brown stigma. The large square cell *1st* $M_2$ is a conspicuous feature of the venation (Plate XXXIII, 44).

## Genus **Toxorhina** Loew

1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683.
1851 *Toxorhina* Loew. Linnaea Entomol., vol. 5, p. 400.
1869 *Toxorrhina* O. S. Mon. Dipt. N. Amer., part 4, p. 109–114.

The small genus Toxorhina includes about nine described species, most of which are from tropical America. The exceedingly reduced radial sector is the most interesting characteristic of the adult. The larval

life is spent presumably in damp earth, a very different habitat from that of the closely related genus Elephantomyia. The following key divides the local species:

Cell *1st* $M_2$ closed; body coloration brownish yellow; size, wing 6.5 mm. [*Toxorrhina magna* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 232. 1865.] (Plate XXXIII, 45.) *T. magna* (O. S.)

Cell *1st* $M_2$ open by the atrophy of the medial cross-vein (closed in abnormal specimens only); body coloration gray; size smaller, wing less than 5.5 mm. [*Toxorrhina muliebris* O. S. Proc. Ent. Soc. Phila., p. 233. 1865.] (Plate XXXIII, 46.) . . *T. muliebris* (O. S.)

The small *T. muliebris* is northern in its distribution, while the larger *T. magna* is much more southern.

## Genus **Atarba** Osten Sacken

1869 *Atarba* O. S. Mon. Dipt. N. Amer., part 4, p. 127–128.

A small number of species (about eight) are included in the genus Atarba, most of them belonging to tropical South America. In many of the species, including the local *A. picticornis*, the antennae of the male are elongated and beautifully annulated with yellow and brown. As has already been pointed out by the author a number of times, many of the species of crane-flies described by various workers as species of Atarba are in reality members of the aberrant eriopterine genus Gonomyia, subgenus Leiponeura (Alexander, 1916:508–509).

### *Atarba picticornis* O. S.

1869 *Atarba picticornis* O. S. Mon. Dipt. N. Amer., part 4, p. 128–129, pl. 1, fig. 13.

*Atarba picticornis* is a rather common species, in suitable localities, flying in late June and July. The adult is reddish yellow; the antennae are yellow with the apical half of each flagellar segment dark brown; the abdomen is yellow with a black ring before the tip; the wings are pale yellow. *Sc* is short, the cross-vein *r* lacking; cell *1st* $M_2$ is small, with the basal deflection of $Cu_1$ inserted at its base (Plate XXXIII, 47).

## Genus **Antocha** Osten Sacken

1859 *Antocha* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

The small genus Antocha includes about seven described species in the Northern Hemisphere. The immature stages are strictly aquatic, the pupae having branched pronotal breathing horns as in Simulium.

Both larvae and pupae live in cases on rocks, often in very rapid water, and the larvae are very pediciine in appearance. Mating takes place on the stones along the streams in which the larvae live.

*Antocha saxicola* O. S.

1859 *Antocha saxicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.
1859 *Antocha opalizans* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

*Antocha saxicola* is a common fly, which may be mistaken only for a Dicranomyia but is readily distinguished by the very prominent anal angle of the wings (Plate XXXIII, 48), an uncommon feature in crane-flies. The milky-white color of the wings, and the very long, straight sector, are noteworthy characters. There are two distinct color phases which may represent distinct species when better known. The gray form has been described as *A. saxicola*, the red form as *A. opalizans*.

Genus **Dicranoptycha** Osten Sacken

1818 *Marginomyia* Meig. Syst. Beschr., vol. 1, p. 147.
1859 *Dicranoptycha* O. S. Proc. Acad. Nat. Sci. Phila., p. 217.

There are about nine described species of Dicranoptycha, six from North America, two from Europe, and one from Africa. *D. signaticollis* v. d. W. (of Java) is a Libnotes. The immature stages are spent in rather dry soil in open woods.

The following key separates the local species of Dicranoptycha:

1. Large, wing over 10 mm.; wings deep reddish brown, the veins with short golden hairs; *Rs* elongate, nearly twice the length of cell *1st* $M_2$. [Proc. Acad. Nat. Sci. Phila., p. 217. 1859.] (Plate XXXIII, 49.) ..... *D. germana* O. S.
   Smaller, wing under 9 mm.; wings light gray or yellowish subhyaline; *Rs* shorter, about as long as or only slightly longer than cell *1st* $M_2$ ..... 2
2. Body coloration brownish gray; wings suffused with gray. [Proc. Acad. Nat. Sci. Phila., p. 218, pl. 4, fig. 13. 1859.] (Plate XXXIII, 51.) ..... *D. sobrina* O. S.
   Body coloration pale yellow; wings pale yellow. [Proc. Acad. Nat. Sci. Phila., p. 500–501, pl. 25, fig. 12. 1916.] (Plate XXXIII, 50.) ..... *D. winnemana* Alex.

There are three additional Austral species that may occur within the faunal limits considered by this paper. Of these, *Dicranoptycha nigripes* O. S. and *D. minima* Alex. have the tips of the femora blackened; *D. tigrina* Alex. resembles *D. sobrina*, but has the abdomen conspicuously cross-banded with brown and yellow, not uniformly brown as in *sobrina*.

A conspicuous feature occurring in the flies of this genus is the presence of a fold in the first anal cell of the wing, which is most evident if the wing is held against the light.

### Genus **Teucholabis** Osten Sacken

1859 *Teucholabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

There are about forty-five described species in the genus Teucholabis, two-thirds of which are from tropical America, the center of distribution for the group. The larvae of *T. complexa* are found underneath decaying bark, a habitat very like that of the related genus Elephantomyia.

The local species of Teucholabis may be separated according to the following key:

Wing over 6 mm.; wings broad; *Sc* long, ending beyond two-thirds the length of the sector; *r* inserted on $R_{2+3}$; vein $R_{2+3}$ not upturned at its tip, the end of cell *2d* $R_1$ being much broader than the end of cell $R_3$; prescutum reddish with three black stripes. [Proc. Acad. Nat. Sci. Phila., p. 223, pl. 3, fig. 10. 1859.] (Plate XXXIII, 52.) *T. complexa* O. S.

Smaller, wing under 5 mm.; wings narrow; *Sc* short, ending before midlength of the sector; *r* inserted at or near the end of *Rs*; vein $R_{2+3}$ upturned at the tip, the end of cell $R_3$ being broader than the end of cell *2d* $R_1$; prescutum shiny black, only the humeral parts of the sclerite light yellow. [Can. Ent., vol. 48, p. 43. 1916. Proc. Acad. Nat. Sci. Phila., p. 498, pl. 25, fig. 16. 1916.] (Plate XXXIII, 53.) ..... *T. lucida* Alex.

The vigorous, broad-winged *T. complexa* is the northernmost local species.

## Tribe **Eriopterini**

The genera of the tribe Eriopterini may be separated in accordance with the following key:

1. Wings very much reduced, microscopic, very much smaller than the halteres. *Chionea* Dalman (p. 902)
   Wings normally developed, much longer than the halteres ..... 2
2. Three branches of the media reaching the wing margin ..... *Cladura* O. S. (p. 903)
   Two branches of the media reaching the wing margin ..... 3
3. $R_2$ shorter than $R_{2+3}$ ..... 4
   $R_2$ longer than $R_{2+3}$ ..... 7
4. Radial cross-vein present ..... 5
   Radial cross-vein lacking ..... 6
5. *Rs* elongate, longer than $R_{4+5}$ alone; tuberculate pits on the anterior part of the prescutum ..... *Rhabdomastix caudata* (Lundb.) (p. 904)
   *Rs* shorter, not so long as $R_{4+5}$; tuberculate pits retreated back on the prescutum. *Erioptera*, subgenus *Empeda* (p. 908)
6. *Sc* very long, extending to the end of the sector; basal deflection of $Cu_1$ at the fork of *M* or beyond ..... *Rhabdomastix* Skuse (p. 904)
   *Sc* short, not extending beyond midlength of the sector; if *Sc* projects beyond the base of the sector, the basal deflection of $Cu_1$ is far before the fork of *M*. *Gonomyia* Meig. (p. 904)

7. *Rs* long, normal in position; cell *1st* $R_1$ elongated.....8
*Rs* shortened, its first fork with vein $R_{2+3}$ at an angle to the end of the sector so that cell *1st* $R_1$ is equilateral or nearly so.....*Cryptolabis* O. S. (p. 906)
8. *Rs* ending in cell $R_2$.....*Molophilus* Curt. (p. 906)
*Rs* ending in cell $R_3$.....9
9. A supernumerary cross-vein in cell $R_2$; second anal vein strongly bisinuate. *Helobia* St. Farg. et Serv. (p. 907)
No supernumerary cross-vein in cell $R_2$; second anal vein not bisinuate.....10
10. $Cu_1$ tending to turn toward the wing apex; forks of the longitudinal veins very long and deep.....*Erioptera* Meig. (p. 908)
$Cu_1$ straight or tending to turn away from the wing apex.....11
11. Sides of the long cell *1st* $M_2$ parallel; $Sc_2$ not far removed from the tip of $Sc_1$; coloration of the local species black; basal deflection of $Cu_1$ beneath the middle of cell *1st* $M_2$. *Gnophomyia* O. S. (p. 909)
Sides of cell *1st* $M_2$ more or less divergent distad; $Sc_2$ retreated toward the wing base so that $Sc_1$ is usually more than two-thirds the length of the sector.....12
12. Deflection of $Cu_1$ meeting $M$ far before the fork of the latter; *Rs* long and straight at its origin; the terminal three segments of the antennae abruptly smaller than the other segments of the flagellum; wings glabrous.....*Trimicra* O. S. (p. 910)
Deflection of $Cu_1$ meeting $M$ usually at the fork or on $M_{3+4}$ underneath cell *1st* $M_2$; *Rs* shorter, tho straight; flagellar segments of the antennae gradually and uniformly smaller toward the tip of the organ; wings pubescent.....*Ormosia* Rond. (p. 911)

## Genus **Chionea** Dalman

1816 *Chionea* Dalman. K. Vet. Akad. Handl., vol. 1, p. 102.

Chionea is a peculiar genus of subapterous crane-flies. There are about five European and six American species so far described. The possible evolution of the group from winged ancestors (Pterochionea Alex., Crypteria Berg.) has been discussed by the author in another paper (Alexander, 1916:529–530).

The immature stages of the known species are spent in the soil. The adult flies are usually found crawling about on the snow, being more conspicuous when snow is on the ground than at other seasons. In the spring and fall they are occasionally found in leaf mold. An interesting paper on the genus has been written by Johnson (1907). Dr. Dietz has in his collection a female specimen which was taken at Aweme, Manitoba, in September, when the temperature was below zero.

All the earlier authors describe this fly as being wingless. This is not exactly true, however, the wings being present tho reduced to mere knobs, much smaller than the halteres. The generalized species have the normal number of antennal segments for this tribe of flies, this being sixteen — the two scapal segments, a basal fusion segment of the flagellum made up of five segments, and nine free flagellar segments beyond. In the

specialized forms the number of free segments beyond the fusion segment is reduced to four or five, making a total of eleven or twelve segments.

The following key separates the local species of Chionea:

1. Color of the body grayish. [Can. Ent., vol. 49, p. 205–206. 1917.]
*C. noveboracensis* Alex.

Color of the body reddish yellow or yellow ..... 2

2. Form long and slender, length of male less than 4 mm., diameter across thorax about 0.6 mm.; legs all very long and slender, not incrassated. [Can. Ent., vol. 49, p. 206. 1917.] ..... *C. gracilis* Alex.

Form stouter, length of male over 4 mm., diameter across thorax over 1 mm.; male with at least the posterior legs incrassated ..... 3

3. Antennae with 12 segments, there being 9 flagellar segments beyond the 1st, or fusion, segment; all the femora incrassated; size larger, length of male about 5.5 mm., diameter across thorax 1.5 mm. [Can. Ent., vol. 49, p. 204–205. 1917.] ..... *C. primitiva* Alex.

Antennae with 7 segments, there being 4 flagellar segments beyond the 1st, or fusion, segment; only the hind femora incrassated; size smaller, length of male about 5 mm., diameter across thorax 1 mm. [Ins. Injur. to Veget., 3d ed., p. 601, fig. 260. 1841.]
*C. valga* Harr.

(*C. scita* Walk. and *C. aspera* Walk. are probably synonymous with *C. valga*.)

## Genus **Cladura** Osten Sacken

1859 *Cladura* O. S. Proc. Acad. Nat. Sci. Phila., p. 229.

There are but two described species of Cladura, both occurring within the limits considered in this paper. *Cladura fuscula* Loew (of Europe) is *Adelphomyia senilis* (Hal.); *C. flavescens* Brun. (of India) is doubtfully a member of this genus. It should be noted here that the antennae of Cladura have the basal segments of the flagellum united into a fusion-segment so that the antenna seems to have less than sixteen segments. The immature stages are quite unknown but are presumably spent in the soil.

The two species of Cladura are separated by the following key:

Large species, wing of female over 7 mm.; reddish yellow, the thoracic pleura spotted with brown; wings yellowish, the cross-veins and deflections of veins clouded with brown; *Sc* long, ending opposite the base of $R_2$, $Sc_2$ being about opposite the fork of $R_{2+3}$; *r* at or beyond one-third the length of $R_2$; petiole of cell $M_1$ short, not much longer than *m*. [*C. flavoferruginea* O. S., Proc. Acad. Nat. Sci. Phila., pl. 4, fig. 34, 1859. *C. indivisa* O. S., Proc. Acad. Nat. Sci. Phila., p. 291, 1861.] (Plate XXXVII, 102.)
*C. flavoferruginea* O. S.

Smaller species, wing of female under 6 mm.; pale yellow, no spots on the thoracic pleura; wings hyaline without dark markings on the cross-veins and deflections of veins; *Sc* short, ending about opposite midlength of $R_{2+3}$, $Sc_2$ being nearly opposite the fork of the sector; *r* at about one-fourth the length of $R_2$; petiole of cell $M_1$ long, about twice the length of *m*. [Proc. Acad. Nat. Sci. Phila., p. 589–590, pl. 27, fig. 27. 1914.] (Plate XXXVII, 103.)
*C. delicatula* Alex.

These species are characteristic late summer and autumnal crane-flies, very common in some localities thruout September and October. They

frequent open woodlands and shrubbery often remote from running water. *C. delicatula* is apparently a more local species than *C. flavoferruginea*, being more frequently found in mountainous localities.

It should be noted that *C. indivisa* is a synonym of *C. flavoferruginea* O. S. The remarkable variation in the venation of this species has been discussed by Alexander and Leonard (1912).

## Genus **Rhabdomastix** Skuse

1889 *Rhabdomastix* Skuse. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, p. 829, pl. 22, fig. 15.

### (Subgenus **Sacandaga** Alexander)

1911 *Sacandaga* Alex. Ent. News, vol. 22, p. 349–351.

Rhabdomastix is a small genus, including seven described species. The group is close to Gonomyia, but the male hypopygium has a very different structure and is of a distinctly primitive type. The subgenus Rhabdomastix, *sens. str.*, which occurs in Australia and South America, has greatly elongated antennae in the male sex; the subgenus Sacandaga, with four species and a race, has the antennae short in both sexes.

A key to the local species of Rhabdomastix follows:

Cross-vein *r* present tho weak; veins issuing from the small pentagonal cell *1st* $M_2$ subparallel; basal deflection of $Cu_1$ at the fork of *M*; body coloration grayish; arctic species. [*Goniomyia* (*Empeda*) *caudata* Lundb. Vidensk. Meddel. fra den naturh. Foren., p. 267, pl. 6, fig. 18. 1898.] (Plate XXXVI, 96.) ..... *R. caudata* (Lundb.)

Cross-vein *r* lacking; veins issuing from the hexagonal cell *1st* $M_2$ arcuated; basal deflection of $Cu_1$ under the middle of cell *1st* $M_2$; body coloration yellowish. [*Sacandaga flava* Alex. Ent. News, vol. 22, p. 351–352, figs. 1–3. 1911.] (Plate XXXVI, 97.) . . . *R. flava* (Alex.).

## Genus **Gonomyia** Meigen

1818 *Gonomyia* Meig. Syst. Beschr., vol. 1, p. 146.
1869 *Goniomyia* O. S. Mon. Dipt. N. Amer., part 4, p. 176.

In the genus Gonomyia there are about seventy-five described species, which are well distributed thruout the world, being found on all the continents and on many of the oceanic islands. The writer places the species in four subgenera — *Gonomyella* Alex., *Gonomyia* Meig., *Ptilostena* Bergr., and *Leiponeura* Skuse, the second and the fourth occurring within the limits considered in this paper. The coloration of many of the species is often contrasted brown and yellow, the pleura of the thorax being striped longitudinally. The immature stages of the species so far as

known are spent in wet earth or sand, and the larvae are of the usual elongate type of the Eriopterini.

The local species of Gonomyia may be separated according to the following key:

1. Two branches of the radial sector reaching the wing margin. (Subgenus *Leiponeura* Skuse.) ..... 2
   Three branches of the radial sector reaching the wing margin.) Subgenus *Gonomyia* Meig.) ..... 4
2. Outer deflection of vein $M_3$ absent, the cell *1st* $M_2$ being open; costa conspicuously china-white; legs banded with white. [*Elliptera alexanderi* Johns. Psyche, vol. 19, p. 3, fig. 6. 1912.] (Plate XXXVI, 86.) ..... *G. alexanderi* (Johns.)
   Outer deflection of vein $M_3$ present, closing the cell *1st* $M_2$; costa not china-white; legs not banded with white ..... 3
3. Pleural stripes conspicuous; stigma of the wings distinct; femora tipped with dark brown. [Proc. Acad. Nat. Sci. Phila., p. 587–588; pl. 27, fig. 25, wing; pl. 26, fig. 21, hypopygium. 1914.] (Plate XXXVI, 87.) ..... *G. sacandaga* Alex.
   Pleural stripes lacking; no stigmal spot on the wings; femora not tipped with brown. [*Goniomyia manca* O. S. Mon. Dipt. N. Amer., part 4, p. 178–179. 1869.] (Plate XXXVI, 88.) ..... *G. manca* (O. S.)
4. Basal deflection of $Cu_1$ far before the fork of $M$; subcosta long, ending beyond the origin of the sector ..... 5
   Basal deflection of $Cu_1$ at or beyond the fork of $M$; subcosta short, ending opposite or before the origin of the sector ..... 6
5. Wings clear, unspotted. [Ent. News, vol. 26, p. 170–172, figs. 1–3. 1915.] (Plate XXXVI, 89.) ..... *G. mathesoni* Alex.
   Wings spotted. [Proc. Acad. Nat. Sci. Phila., p. 231, pl. 4, fig. 16. 1859.] (Plate XXXVI, 90.) ..... *G. blanda* O. S.
6. Antennae orange at the base, the flagellum dark ..... 9
   Antennae black thruout ..... 7
7. Cell *1st* $M_2$ closed; femora with a dark brown subterminal ring. [Proc. Acad. Nat. Sci. Phila., p. 230. 1859.] (Plate XXXVI, 91.) ..... *G. sulphurella* O. S.
   Cell *1st* $M_2$ open; femora without a dark subterminal ring ..... 8
8. Male hypopygium with the dorsal angle of the pleurite stout, with numerous (about 15) slender hairs; ventral appendage simple, stout, tipped with a blunt black spine; second appendage a powerful, curved, subchitinized arm directed proximad. [Can. Ent., vol. 48, p. 316–317. 1916.] (Plate XXXVI, 92.) ..... *G. florens* Alex.
   Male hypopygium with the dorsal angle of the pleurite slender, with a few (about 10) stout hairs; ventral appendage bifid, the arm with a long, slender, black spine at the tip; second appendage a slender, pale arm that is almost straight, and with two hairs at the tip. [Proc. Acad. Nat. Sci. Phila., p. 230, pl. 4, fig. 17. 1859.] (Plate XXXVI, 93.) ..... *G. cognatella* O. S.
9. Subcosta short, ending before the origin of the sector, the distance between its tip and the origin of the sector being about equal to the *r-m* cross-vein; vein $R_2$ oblique, a little longer than the *r-m* cross-vein; male hypopygium with the gonapophyses and the penis guard fused into a large, prominent, cylindrical tube: thoracic pleura indistinctly striped. [Can. Ent., vol. 48, p. 319–320. 1916.] (Plate XXXVI, 94.) ..... *G. novebarracensis* Alex.
   Subcosta longer, ending about opposite the origin of the sector; vein $R_2$ elongate; male hypopygium with the gonapophyses and the penis guard not fused into a cylindrical tube; thoracic pleura without stripes. [Proc. Acad. Nat. Sci. Phila., p. 231. 1859.] (Plate XXXVI, 95.) ..... *G. subcinerea* O. S.

The above key is adapted from a revision of the American species of the genus by the author (Alexander, 1916: 508–528).

## Genus **Cryptolabis** Osten Sacken

1859 *Cryptolabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 224.

Cryptolabis is a small but well-defined genus, including three species, of which two are Nearctic and one is Neotropical. Nothing is known of the immature stages, but those of *C. paradoxa*, at least, are probably spent in moist earth.

### *Cryptolabis paradoxa* O. S.

1859 *Cryptolabis paradoxa* O. S. Proc. Acad. Nat. Sci. Phila., p. 225, pl. 4, figs. 14, 15, 15 a.

The species *Cryptolabis paradoxa*, a curious little fly, is dark brown, with the dorso-pleural membranes and the root of the wings more yellowish; the whitish wings, with the apical cells pubescent and the sector short and straight or even slightly convex (Plate XXXVII, 101), easily distinguish the species. It is often rather common on rank herbage growing along wide creeks or on river banks. In these situations it may be swept in numbers from late June thruout July.

## Genus **Molophilus** Curtis

1833 *Molophilus* Curt. Brit. Entomol., p. 444.

The genus Molophilus includes about forty-five described species, found in most parts of the world but better represented, apparently, in the temperate regions of both hemispheres. The immature stages so far as known are spent in moist earth.

The local species of Molophilus may be separated according to the following key:

1. Size very small, wing about 2.5 mm.; basal deflection of $R_{2+3}$ short, perpendicular, about as long as the radial cross-vein; basal deflection of $Cu_1$ far before the fork of *M.* [*Erioptera ursina* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 70.) ..... *M. ursinus* (O. S.)

   Size larger, wing over 2.6 mm.; basal deflection of $R_{2+3}$ longer, oblique; basal deflection of $Cu_1$ near the fork of *M* (as in *M. nova-caesariensis*) or beyond it on $M_{3+4}$ . . . 2

2. Wings with a brown spot on the basal deflection of $M_3$. [*Erioptera comata* Doane. Journ. N. Y. Ent. Soc., vol. 8, p. 188, pl. 7, fig. 20. 1900.] (Plate XXXIV, 69.)

   Wings without such a brown spot ..... *M. comatus* (Doane)

3. Antennae of the male elongated; coloration largely yellowish ..... 3

   Antennae short in both sexes; coloration brown or blackish ..... 5

4. Size small, wing under 5 mm.; bright yellow, the abdomen yellow; antennae of the female short. [*Erioptera pubipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 66.).....*M. pubipennis* (O. S.)
   Size larger, wing over 5.3 mm.; abdomen dark brown; antennae of the female longer. [Proc. Acad. Nat. Sci. Phila., p. 505–506, pl. 27, fig. 37. 1916.] (Plate XXXIV, 67.) *M. fultonensis* Alex.
5. Size small, wing under 3.5 mm.; basal deflection of $Cu_1$ near the fork of *M*. [Proc. Acad. Nat. Sci. Phila., p. 506–507, pl. 27, fig. 38. 1916.] (Plate XXXIV, 68.) *M. nova-caesariensis* Alex.
   Size larger, wing over 4 mm.; basal deflection of $Cu_1$ beyond the fork of *M* on $M_{3+4}$.....6
6. Antennae dark-colored; body coloration grayish brown. [*Erioptera hirtipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 65.) *M. hirtipennis* (O. S.)
   Antennae with the basal segments pale; body coloration pale brown. [*Erioptera forcipula* O. S. Mon. Dipt. N. Amer., part 4, p. 163. 1869.].....*M. forcipula* (O. S.)

The species identified above as being *M. comatus* may not belong to this species, which was described from western North America. The writer has seen only females (from Maine), but he has compared this material with Doane's types (also females) and cannot separate the material on the female sex.

## Genus **Helobia** St. Fargeau et Serville

1825 *Helobia* St. Farg. et Serv. Encyclop. Method., Ins., vol. 10, p. 585.
1830 *Symplecta* Meig. Syst. Beschr., vol. 6, p. 282.
1865 *Idioneura* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 615.
1886 *Symplectomorpha* Mik. Wien. Ent. Zeitung, vol. 5, p. 318.

In the genus Helobia there are four described species, one of which, the local *H. hybrida*, is probably the most widely distributed of all crane-flies, ranging from India over Europe and Asia, thruout North America, and southward along the Andes to Chile and Argentina. Future collecting will undoubtedly extend the range even more. The immature stages are spent in moist earth and sand.

### *Helobia hybrida* (Meig.)

1804 *Limonia hybrida* Meig. Klass., vol. 1, p. 57, pl. 3, fig. 17.
1818 *Limnobia punctipennis* Meig. Syst. Beschr., vol. 1, p. 147, pl. 5, figs. 2, 3, 7.
1848 *Limnobia cana* Walk. List Dipt. Brit. Mus., vol. 1, p. 48.

*Helobia hybrida* is a grayish fly, with three brown stripes on the prescutum; the wings are whitish, with a supernumerary cross-vein in cell $R_2$ and the second anal vein curiously bisinuate (Plate XXXVII, 98). The species is common everywhere. It is the earliest of the vernal

crane-fly fauna, appearing on the wing in March. It is seen most commonly in spring and autumn, and is less numerous in July. It is presumably double-brooded.

## Genus **Erioptera** Meigen

1800 *Polymeda* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Erioptera* Meig. Illiger's Mag., vol. 2, p. 262.
1856 *Chemalida* Rond. Prodromus, vol. 1, p. 180.
1856 *Limnaea* Rond. Prodromus, vol. 1, p. 181.
1861 *Limnoica* Rond. Prodromus, vol. 4, Corrigenda, p. 11.

The rather extensive genus Erioptera includes about ninety described species, most numerous in the Northern Hemisphere. The immature stages of the known species are spent in damp earth. The local species are distributed in five subgenera, separated by the following key:

1. Second anal vein arcuated so that cell *1st A* is as broad at the middle as, or broader than, at the margin; cross-vein *m* absent, cell *1st* $M_2$ opening into cell $M_2$ . . . . . *Erioptera* Meig.
   Anal veins divergent, cell *1st A* being broadest at the margin; cell *1st* $M_2$ closed, if open the outer deflection of $M_3$ lacking, cell *1st* $M_2$ opening into cell $M_3$ (except in Empeda) . . . . . 2
2. Fork of cell $R_2$ short, about as long as its petiole ($R_{2+3}$); $Sc_1$ short . . . . . *Empeda* O. S.
   Fork of cell $R_2$ long, at least four times as long as its petiole ($R_{2+3}$); $Sc_1$ longer . . . . . 3
3. Cell *1st* $M_2$ open, the outer deflection of $M_3$ atrophied; if closed, the cross-vein *m* and the deflection of $M_3$ about on a line . . . . . *Mesocyphona* O. S.
   Cell 1st $M_2$ closed . . . . . 4
4. A spur from the outer deflection of $M_3$ jutting into cell *1st* $M_2$ . . . . . *Hoplolabis* O. S.
   No spur from $M_3$ jutting into cell *1st* $M_2$ . . . . . *Acyphona* O. S.

The following key divides the local species of Erioptera:

1. Cell *1st* $M_2$ open by the atrophy of the outer deflection of $M_3$. (Subgenus *Mesocyphona*.) . . . . . 2
   Cell *1st* $M_2$ closed; if open, it is by the atrophy of the medial cross-vein . . . . . 4
2. Wings pale gray, with small brown dots at the tips of the veins along the margins. [Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXV, 79.) . . . . . *E. parva* O. S.
   Wings grayish or brown, with white dots and spots . . . . . 3
3. Wings with abundant white dots in all the cells; each femur with two brown rings. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 17. 1823.] (Plate XXXV, 77.) *E. caloptera* Say
   Wings with about twenty large spots that are confined to the region of the veins; each femur with a single brown ring before the tip. [Can. Ent., vol. 50, p. 383–384. 1918.] (Plate XXXV, 78.) . . . . . *E. needhami* Alex.
4. Cell *1st* $M_2$ open by the atrophy of *m*; second anal vein arcuated, before its tip bent strongly toward the first so that cell *1st A* at its middle is about as broad as or broader than at the margin. (Subgenus *Erioptera*.) (See also *E.* [*Empeda*] *stigmatica*, below.) . 5
   Cell *1st* $M_2$ closed; anal veins divergent . . . . . 10
5. Knobs of the halteres dark brown. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 72.) . . . . . *E. septemtrionis* O. S.
   Knobs of the halteres pale . . . . . 6

6. Body and wings dark brown. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 71.) ..... *E. villosa* O. S.
Body and wings yellow or green ..... 7
7. Wings yellowish, the cross-veins and deflections of veins with tiny brown dots. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 74.) ..... *E. chrysocoma* O. S.
Wings yellowish or green, unmarked ..... 8
8. Thorax reddish, the humeral parts of the mesonotum yellow; eyes of the male conspicuously enlarged. [Proc. Acad. Nat. Sci. Phila., p. 226, pl. 4, fig. 19. 1859.] (Plate XXXV, 73.) ..... *E. vespertina* O. S.
(*E. megophthalma* Alex. [Can. Ent., vol. 50, p. 60–61, 1918], described since the above was written, is entirely reddish without the yellow humeral angles to the thorax.)
Thorax pale green or yellow; eyes of both sexes normal ..... 9
9. Coloration of body and wings pale green. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 75.) ..... *E. chlorophylla* O. S.
Coloration of body and wings pale yellow. [Mon. Dipt. N. Amer., part 4, p. 157. 1869.] (Plate XXXV, 76.) ..... *E. straminea* O. S.
10. Cell $R_2$ short, about as long as $R_{2+3}$ alone. (Subgenus *Empeda*.) ..... 11
Cell $R_2$ deep, much longer than $R_{2+3}$ alone ..... 12
11. Cell *1st* $M_2$ closed. [Proc. Acad. Nat. Sci. Phila., p. 503–505, pl. 27, fig. 36. 1916.] (Plate XXXV, 84.) ..... *E. nyctops* Alex.
Cell *1st* $M_2$ open. [*Empeda stigmatica* O. S. Mon. Dipt. N. Amer., part 4, p. 184. 1869.] (Plate XXXV, 85.) ..... *E. stigmatica* (O. S.)
12. A stump of a vein in cell *1st* $M_2$; no brown bands on the femora. (Subgenus *Hoplolabis*.) [Proc. Acad. Nat. Sci. Phila., p. 227, pl. 4, figs. 20, 21. 1859.] (Plate XXXV, 83.) ..... *E. armata* O. S.
No stump of a vein in cell *1st* $M_2$; femora banded with brown. (Subgenus *Acyphona*.) ..... 13
13. Wings with a broad brown band at the cord and a large brown basal spot. [Proc. Acad. Nat. Sci. Phila., p. 227, pl. 4, fig. 23. 1859.] (Plate XXXV, 80.) ..... *E. venusta* O. S.
Wings not so marked ..... 14
14. Coloration of body and wings more yellowish; an uninterrupted brown band along the cord; brown bands on the femora less extensive, the yellow area between them broad; basal deflection of $Cu_1$ at the fork of *M*. [Mon. Dipt. N. Amer., part 4, p. 158. 1869.] (Plate XXXV, 81.) ..... *E. armillaris* O. S.
Coloration of body and wings more brownish, the markings on the wings less extensive and the band on the cord interrupted; bands on the femora very extensive, the yellowish area between them very narrow; basal deflection of $Cu_1$ before the fork of *M*. [Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXV, 82.) ..... *E. graphica* O. S.

*Erioptera* (*Empeda*) *noctivagans* Alex. (Alexander, 1917:200–201), from Virginia, has been described since the completion of the above key. It is closest to *E. stigmatica*, but is larger and darker, the wing veins are dark brown with an indistinct darker seam along the cord, and the three pleural appendages of the male hypopygium are very unequal in length, the shortest being less than two-thirds the length of the longest and conspicuously bifid at its apex. The very long verticils of the antennae in the subgenus Empeda are present, but are less conspicuous than in *E. stigmatica*.

## Genus **Gnophomyia** Osten Sacken

1859 *Gnophomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.
1867 *Furina* Jaenn. Abhandl. Senkenb. Ges., vol. 6, p. 318.

The genus Gnophomyia includes about twenty-eight species of medium-sized to comparatively large flies, mostly from tropical America. The immature stages so far as known are spent beneath the decaying bark of deciduous trees (Liriodendron, Populus, Acer, and others).

*Gnophomyia tristissima* O. S.

1859 *Gnophomyia tristissima* O. S. Proc. Acad. Nat. Sci. Phila., p. 224, pl. 4, fig. 18.

*Gnophomyia tristissima* is a rather small blackish fly, with dark wings and the knobs of the halteres bright yellow. The venation is as shown in Plate XXXVII, 100.

A second species of the genus, *Gnophomyia luctuosa* O. S. (Proc. Acad. Nat. Sci. Phila., p. 224, 1859), has recently been taken near Washington, D. C., by Mr. Shannon. It is a southern species, with a wide range over Central America and northern South America. It may be readily distinguished from *G. tristissima* by its stouter build, entirely black halteres, and apically pubescent wings.

Genus **Trimicra** Osten Sacken

1861 *Trimicra* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

The genus Trimicra includes about fourteen described species of rather inconspicuously colored flies of medium size. The species are found in all the principal regions of the globe, including many of the oceanic islands. The genotype, *Trimicra anomala*, was later considered by its describer as being the same as the European *T. pilipes* Fabr., but the two should be regarded as being distinct species until the question can be settled by the study of ample material. The immature stages are spent in moist earth.

*Trimicra anomala* O. S.

1861 *Trimicra anomala* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

*Trimicra anomala* is a brownish gray fly. The prescutum has three dark brown stripes, and the abdominal segments are margined laterally and caudally with paler. The wings (Plate XXXVII, 99) are suffused with pale brown, the cross-veins being a little darker. The legs and the body are clothed with long, erect hairs. The species is more numerous southward and westward.

## Genus **Ormosia** Rondani

1856 *Ormosia* Rond. Prodromus, vol. 1, p. 180.
1856 *Ilisomyia* Rond. Prodromus, vol. 1, p. 180.
1860 *Rhypholophus* Kol. Wien. Ent. Monatschr., vol. 4, p. 393.
1863 *Dasyptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.

The genus Ormosia includes about sixty-two described species, of temperate zones, almost all occurring in the temperate regions of Europe and North America. The immature stages are spent in mud and damp earth.

The local species of Ormosia may be separated in accordance with the following key:

1. Wings spotted or clouded with darker ..... 2
   Wings unicolorous or nearly so, the stigma only being darker ..... 5
2. Anal veins divergent; wing markings produced by actual dark brown spots and blotches ..... 3
   Anal veins convergent, the second anal vein before its tip bent strongly toward the first; wing markings produced by dark-colored hairs on pale brown clouds ..... 4
3. Wings with brown dots in all the cells. [*Rhypholophus innocens* O. S. Mon. Dipt. N. Amer., part 4, p. 142. 1869.] (Plate XXXIV, 56.) ..... *O. innocens* (O. S.)
   Wings with three brown costal spots, the cord margined with brown, the base and the apex of the wing darkened. [Psyche, vol. 18, p. 200–201, pl. 16, fig. 6. 1911.] (Plate XXXIV, 55.) ..... *O. apicalis* Alex.
   (*O. atriceps* Dietz [Trans. Amer. Ent. Soc., vol. 42, p. 136–137, pl. 10, figs. 1 and 2, 1916] is apparently too close to *O. apicalis* to be separated therefrom.)
4. An indistinct crossband along the cord. [*Erioptera fascipennis* Zett. Ins. Lapponica, Dipt., p. 831. 1838.] ..... *O. fascipennis* (Zett.)
   Wings with three or four indistinct grayish crossbands. [*Erioptera nubila* O. S. Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXIV, 54.) ..... *O. nubila* (O. S.)
5. Cell *1st* $M_2$ closed ..... 6
   Cell *1st* $M_2$ open ..... 10
6. Anal veins divergent ..... 7
   Second anal vein arcuated, before its tip bent strongly toward the first. [*Rhypholophus arcuatus* Doane. Ent. News, vol. 19, p. 201. 1908.] ..... *O. arcuata* (Doane)
7. Antennae entirely brown; thorax reddish brown, shining; basal deflection of $Cu_1$ under the middle of cell *1st* $M_2$. [Trans. Amer. Ent. Soc., vol. 42, p. 137–138, pl. 10, fig. 3. 1916.] ..... *O. abnormis* Dietz
   Not colored as above; basal deflection of $Cu_1$ before or at the fork of $M$ ..... 8
8. Entire thorax and coxae yellowish red; antennae pale yellowish, darkened toward the tip. [Trans. Amer. Ent. Soc., vol. 42, p. 138–139, pl. 10, fig. 4. 1916.] *O. luteola* Dietz
   Thorax not colored as above ..... 9
9. Mesonotum reddish with a median brown line which in some cases is indistinct; antennae pale thruout or with only the extreme tip darkened. [*Trimicra pygmaea* Alex. Psyche, vol. 19, p. 166, pl. 13, fig. 3. 1912.] (Plate XXXIV, 58.) ..... *O. pygmaea* (Alex.)
   (*O. pilosa* Dietz is the same as *O. pygmaea*.)
   Mesonotum brownish gray; the four basal antennal segments yellow. [*Rhypholophus nigripilus* O. S. Mon. Dipt. N. Amer., part 4, p. 142. 1869.] (Plate XXXIV, 57.) *O. nigripila* (O. S.)
10. Medial cross-vein lacking, cell *1st* $M_2$ confluent with cell $M_2$ ..... 11
    Outer deflection of $M_3$ lacking, cell *1st* $M_2$ confluent with cell $M_3$ ..... 12

11. Second anal vein arcuated, before its tip bent strongly toward the first. [*Erioptera holotricha* O. S. Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] ... *O. holotricha* (O. S.)
Anal veins divergent. [Trans. Amer. Ent. Soc., vol. 42, p. 140, pl. 10, fig. 6. 1916.] *O. palpalis* Dietz

12. Antennae of both sexes shorter than the thorax ... 13
Antennae of the male approximately as long as the whole body, beadlike in structure ... 19

13. Second anal vein arcuated, before its tip bent strongly toward the first ... 14
Anal veins divergent ... 18

14. Thorax reddish ... 15
Thorax not reddish ... 16

15. Mesonotum with a dark median line; male hypopygium with two pleural appendages which are almost straight; gonapophyses elongate, black, profoundly bifid; penis guard not trifid. [*Rhypholophus rubellus* O. S. Mon. Dipt. N. Amer., part 4, p. 144, pl. 1, fig. 15. 1869.] (Plate XXXIV, 60.) ... *O. rubella* (O. S.)
Mesonotum without a dark median line; male hypopygium with the pleural appendage a single curved hook; gonapophyses strongly curved, entire hooks; penis guard trifid at apex. [Can. Ent., vol. 49, p. 24–25. 1917.] (Plate XXXIV, 59.) *O. nimbipennis* Alex.

16. Stigma distinct, dark brown, the marking continued down onto the cord. [*Erioptera meigenii* O. S. Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXIV, 61.) *O. meigenii* (O. S.)
Stigma indistinct or lacking ... 17

17. Thorax and antennae light yellow. [*Rhypholophus parallelus* Doane. Ent. News, vol. 19, p. 202. 1908.] ... *O. parallela* (Doane)
Thorax brown, with a grayish pruinosity and a rather broad darker stripe; antennae brown. [Trans. Amer. Ent. Soc., vol. 42, p. 141. 1916.] ... *O. perplexa* Dietz

18. Mesonotum with a darker line on either side; ninth sternite produced into a median spatulate lobe. [Trans. Amer. Ent. Soc., vol. 42, p. 142–143, pl. 10, fig. 8. 1916.] *O. bilineata* Dietz
Mesonotum reddish brown with a median brown stripe; ninth sternite produced into two flattened lobes that project far caudad. [Trans. Amer. Ent. Soc., vol. 42, p. 143–144, pl. 10, fig. 9. 1916.] ... *O. deviata* Dietz

19. Anal veins convergent ... 20
Anal veins divergent ... 21

20. Segments of flagellum shorter, without pale apices. [Can. Ent., vol. 49, p. 25. 1917.] (Plate XXXIV, 63.) ... *O. mesocera* Alex.
Antennal segments elongated, the segments attenuated and the apices pale. [*Rhypholophus monticola* O. S. Mon. Dipt. N. Amer., part 4, p. 145. 1869.] (Plate XXXIV, 62.) ... *O. monticola* (O. S.)

21. Reddish brown; mesonotum with an indistinct brown median stripe. [Trans. Amer. Ent. Soc., vol. 42, p. 144–145, pl. 10, fig. 10. 1916.] ... *O. divergens* Dietz
Dark brown; mesonotum with three darker brown stripes. [Can. Ent., vol. 49, p. 26. 1917.] (Plate XXXIV, 64.) ... *O. megacera* Alex.
(*O. megacera* is probably the same as *O. divergens*, the latter name preoccupied by *O. divergens* Coq. [1905].)

The small flies that make up this characteristic genus are very common, appearing in small swarms under overhanging ledges, along the lower face of an inclined tree, or in similar situations. The early spring species are *Ormosia innocens*, *O. nubila*, *O. meigenii*, *O. holotricha*, and others; *O. apicalis*, *O. megacera*, and *O. mesocera* occur in early summer; *O. nigripila*, *O. nimbipennis*, *O. monticola*, and *O. abnormis* are late

summer species. *O. rubella* has a long flight period, from June to September, and some of the early spring species (as *O. nubila* and *O. meigenii*) reappear in the late summer and in the autumn, apparently being double-brooded.

## Tribe **Limnophilini**

The genera of the tribe Limnophilini may be separated according to the following key:

1. $Sc_2$ before the origin of the sector; antennae 17-segmented; wings pubescent. *Ula* Hal. (p. 913)
   $Sc_2$ beyond the origin of the sector; antennae 16-segmented (apparently with fewer segments in *Adelphomyia cayuga*) ..... 2
2. Wings pubescent, at least apically ..... 3
   Wings glabrous or with microscopic pubescence only ..... 5
3. Pubescence including the entire wing; cell $M_1$ absent ..... *Ulomorpha* O. S. (p. 913)
   Pubescence only on the apical cells of the wing; cell $M_1$ present or lacking ..... 4
4. Small species, wing less than 5.5 mm.; male antennae short ..... *Adelphomyia* Bergr. (p. 914)
   Larger species, wing over 6 mm.; male antennae elongated. *Limnophila*, subgenus *Lasiomastix* O. S. (p. 916)
5. A supernumerary cross-vein in cell *C* ..... *Epiphragma* O. S. (p. 914)
   No supernumerary cross-vein in cell *C* ..... *Limnophila* Macq. (p. 915)

### Genus **Ula** Haliday

1833 *Ula* Hal. Ent. Mag., vol. 1, p. 153.
1864 *Macroptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 224.

The small genus Ula includes about six described species, all being Holarctic except one species from Java. The larval stages of the known species are spent in fungi (Alexander, 1915a: 1–8). The species are subject to considerable variation in the wing pattern, but it now seems that in eastern America there are at least two species, which are divided by the following key:

Antennae elongate in the male; wings dusky, but without a heavy brown pattern. [Mon. Dipt. N. Amer., part 4, p. 277. 1869.] ..... *U. paupera* O. S.
Antennae short in both sexes; wings with the cord and outer end of cell *1st* $M_2$ seamed with brown. [Mon. Dipt. N. Amer., part 4, p. 276. 1869.] (Plate XLI, 164.) *U. elegans* O. S.

### Genus **Ulomorpha** Osten Sacken

1869 *Ulomorpha* O. S. Mon. Dipt. N. Amer., part 4, p. 232.

In the genus Ulomorpha there is but a single described species, agreeing superficially with Ula in the entirely pubescent wings but with $Sc_2$ close at the tip of $Sc_1$. The immature stages are in rich organic earth, and are

very different from those of Ula and closer to those of the subgenus Lasiomastix in the genus Limnophila.

*Ulomorpha pilosella* (O. S.)

1859 *Limnophila pilosella* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1869 *Ulomorpha pilosella* O. S. Mon. Dipt. N. Amer., part 4, p. 233.

*Ulomorpha pilosella* is a shiny, reddish brown fly, with the wings faintly darkened. The sessile or subsessile cell $R_2$ is a well-marked feature of the venation (Plate XLI, 163). The insect is common in cold Canadian woods thruout northeastern North America.

## Genus **Adelphomyia** Bergroth

1891 *Adelphomyia* Bergr. Mittheil. Naturf. Ges. Bern, 1890, p. 134.

The species of the genus Adelphomyia are among the smallest of the Limnophilini. The immature stages of the American species are spent in rich, saturated, organic earth in shady situations. There are two European and three American species thus far described. *Adelphomyia cayuga* and *A. americana* are commonest in late summer; *A. minuta* is a species of late spring and early summer, fairly common in rich Canadian woods, in gorges, and near wooded bogs.

A recent study of the larval head in this genus shows a decided relationship with the tribe Pediciini, and it seems probable that the genus will have to be placed in that tribe despite the very limnophiline appearance of the adults.

The local species of Adelphomyia may be separated by the following key:

1. Cell $M_1$ of wings lacking; coloration of body dark brown; antennae with less than 16 segments, the basal segments of the flagellum fused together. [Pomona Journ., vol. 4, p. 831, fig. B. 1912.] (Plate XLI, 162.) ..... *A. cayuga* Alex.
   Cell $M_1$ of wings present; coloration of body yellow or light yellowish brown; antennae with the basal flagellar segments distinct ..... 2
2. Pubescence in cells of wings sparse; cross-vein *r* not evident; cross-vein *m* short or obliterated by fusion of $M_3$ on $M_{1+2}$; color of body light yellow. [Can. Ent., vol. 43, p. 287–288. 1911.] (Plate XLI, 161.) ..... *A. minuta* Alex.
   Pubescence in cells of wings conspicuous; cross-veins *r* and *m* usually distinct, the former in some cases little evident; color of body yellowish brown. [Pomona Journ., vol. 4, p. 829–830, fig. A. 1912. Ent. News, vol. 22, p. 353–354, fig. 4, as *A. senilis* Hal. of Europe. 1911.] (Plate XLI, 160.) ..... *A. americana* Alex.

## Genus **Epiphragma** Osten Sacken

1859 *Epiphragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Epiphragma is a small genus of handsome flies including about eighteen described species, which are most abundant in the tropics of America. The flies are of medium size and are among the most beautiful in the family, their wing pattern of ocellate spots and bands producing a striking effect. The immature stages are amphibious, the larval life being spent in saturated decaying wood such as ash (Fraxinus) and buttonbush (Cephalanthus), in swampy situations, and in similar habitats.

The following key divides the local species:

Wings with pale brown crossbands which are margined with darker; a brown annulus at the tip of each femur. [*Limnobia fascipennis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 19. 1823.] (Plate XLI, 158.).....*E. fascipennis* (Say)

Wings with an irregular pattern of brown and tawny; a brown annulus before the tip of each femur. [*Limnophila solutrix* O. S. Proc. Acad. Nat. Sci. Phila., p. 238. 1859.] (Plate XLI, 159.).....*E. solutrix* (O. S.)

In many specimens of *Epiphragma fascipennis* the wing bands are more continuous than in the wing shown, there being usually three such bands, the last lying across the wing tip distad of the cord. The wing pattern is strongly suggestive of that of the rare primitive tanyderid *Protoplasa fitchii*, and most of the specimens of the latter that have been located in museums were found pinned among series of *Epiphragma fascipennis*.

## Genus **Limnophila** Macquart

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1861 *Limnomya* Rond. Prodromus, vol. 4, Corrigenda, p. 11.
1888 *Pilaria* Sintenis. Sitzber. Nat.-Ges. Dorpat., vol. 8, p. 398.

Limnophila is one of the largest of the crane-fly genera, the number of described species being between one hundred and ninety and two hundred, of which a quarter occur within the geographical limits considered in this paper. The subgenera into which the genus is divided are here recognized largely for convenience only, some of them being poorly definable. The larval and pupal characters will be found to be much more valuable in delimiting these groups. *Limnophila mundoides* and *L. emmelina* both represent groups which are as well defined as the sub-genera here recognized. Most of the forms of northeastern North America fly during the month of June and are to be found in cold Canadian woodlands. The immature stages of most species of Limnophila are spent in rich, saturated mud or earth.

The local species of Limnophila may be separated in accordance with the following key:

1. Cell $M_1$ of the wings present ..... 2
   Cell $M_1$ of the wings lacking ..... 41
2. A supernumerary cross-vein in cell $R_2$ or in cell $M$ ..... 3
   No supernumerary cross-vein in cell $R_2$ or in cell $M$ ..... 6
3. A supernumerary cross-vein in cell $M$ ..... 4
   A supernumerary cross-vein in cell $R_2$. (Subgenus *Dicranophragma* O. S.) [Proc. Acad. Nat. Sci. Phila., p. 240. 1859.] (Plate XXXIX, 139.) ..... *L. fuscovaria* O. S.
4. Wings interruptedly crossbanded with brown; costal region without equidistant brown blotches; *Rs* spurred at the bend; antennae of male elongated. (Subgenus *Idioptera* Macq.) [Mon. Dipt. N. Amer., part 4, p. 206. 1869.] (Plate XXXVIII, 115.) *L. fasciolata* O. S.
   Wings hyaline or spotted with brown; *Rs* slightly or not at all spurred at the bend; antennae of male short. (Subgenus *Ephelia* Schin.) ..... 5
5. Wings hyaline. [Proc. Acad. Nat. Sci. Phila., p. 591, pl. 25, fig. 2. 1914.] (Plate XXXIX, 138.) ..... *L. johnsoni* Alex.
   Wings spotted; a series of about 6 or 7 large brown blotches along the costal margin. [Proc. Acad. Nat. Sci. Phila., p. 235, pl. 4, fig. 25. 1859.] (Plate XXXIX, 137.) *L. aprilina* O. S.
6. Apical cells of wings pubescent; antennae of male elongated. (Subgenus *Lasiomastix* O. S.) ..... 7
   Apical cells of wings not pubescent ..... 8
7. Thorax shiny black; wings banded with brown. [*Limnobia macrocera* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 20. 1823.] (Plate XXXVIII, 113.) *L. macrocera* (Say)
   Thorax dark gray; wings unmarked. [Mon. Dipt. N. Amer., part 4, p. 208. 1869.] (Plate XXXVIII, 117.) ..... *L. tenuicornis* O. S.
   (*L. subtenuicornis* Alex. [Can. Ent., vol. 50, p. 61–62, 1918], described since this key was made, has cell $M_1$ lacking. It is a member of the subgenus Lasiomastix and is readily distinguished by the combination of pubescent wings and lack of cell $M_1$. There can be no doubt that *L. tenuicornis* and *L. subtenuicornis* should be coupled with *L. macrocera* in the subgenus *Lasiomastix*, both being notable by the distinct pubescence in the apical cells of the wings.)
8. Thorax shiny black ..... 9
   Thorax not shiny black ..... 10
9. Wings with a brownish tinge; femora dull brownish yellow, narrowly tipped with dark brown; legs stout, conspicuously hairy; male hypopygium of the normal simple limnophiline structure. (Subgenus *Prionolabis* O. S.) [Mon. Dipt. N. Amer., part 4, p. 226. 1869.] (Plate XL, 144.) ..... *L. munda* O. S.
   Wings hyaline or nearly so; femora dark brown, only the extreme bases paler; legs slender, not conspicuously hairy; male hypopygium complex in structure. [Journ. N. Y. Ent. Soc., vol. 24, p. 120–121, pl. 8, fig. 3. 1916.] (Plate XL, 145.) *L. mundoides* Alex.
10. Hind tarsi white; antennae of male elongated ..... 11
    Hind tarsi not white ..... 12
11. Thorax black with a gray bloom; $R_{2+3}$ about equal to or slightly longer than the basal deflection of $Cu_1$. [Mon. Dipt. N. Amer., part 4, p. 209. 1869.] (Plate XXXVIII, 118.) ..... *L. niveitarsis* O. S.
    Thorax reddish yellow; $R_{2+3}$ about twice as long as the basal deflection of $Cu_1$. [Ent. News, vol. 24, p. 248–249, fig. 1913.] (Plate XXXVIII, 119.) ..... *L. albipes* Leon.

12. Cross-vein *r* removed some distance from the tip of $R_1$, so that this distance is from one and one-half to two times the length of the radial cross-vein; tuberculate pits present ..... 13
    Ultimate segment of $R_1$ curved to the costa and scarcely longer than the cross-vein *r* itself; tuberculate pits lacking in all species except *fratria* ..... 22
    (*L. marchandi* should be interpreted as coming in this division, from the evident relationship with *L. alleni*.)
13. Cell *1st* $M_2$ very much elongated, the inner end lying far inside the level of the cord. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 124.) ..... *L. areolata* O. S.
    Cell *1st* $M_2$ not greatly elongated, the inner end at the level of the cord ..... 14
14. $R_{2+3}$ longer than cell $R_2$ alone. [Proc. Acad. Nat. Sci. Phila., p. 238, pl. 4, fig. 26. 1859.] (Plate XXXVIII, 127.) ..... *L. ultima* O. S.
    $R_{2+3}$ not longer than cell $R_2$ alone ..... 15
15. Cell $M_1$ very short, not longer than the basal deflection of $Cu_1$. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 125.) ..... *L. brevifurca* O. S.
    (Specimens of *L. brevifurca* are rather frequently found in which the fusion of $M_{1+2}$ is continued to the wing margin, in which case the species would run down to couplet 41; such abnormal specimens are rare, however, and usually have one of the wings normal.)
    Cell $M_1$ long, more than twice as long as the basal deflection of $Cu_1$ ..... 16
16. Head narrow, prolonged behind; cells $R_3$ and *1st* $M_2$ longer than cell $R_5$, so that the cord is not in a straight line; radial and medial veins long, slender, arcuated; second anal vein incurved at the tip. (Subgenus *Pseudolimnophila* Alex.) ..... 17
    Head broad, not narrowed behind; cells $R_3$, $R_5$, and *1st* $M_2$ with their inner ends about on a level; radial and medial veins stout and straight; second anal vein not incurved at the tip. (Subgenus *Eulimnophila* Alex.) ..... 20
17. Wings with small brown dots on the cross-veins and at the forks. [Proc. Acad. Nat. Sci. Phila., p. 236, pl. 4, fig. 24. 1859.] (Plate XXXIX, 135.) ..... *L. luteipennis* O. S.
    Wings clear, unspotted ..... 18
18. Thorax clear blue-gray. [Mon. Dipt. N. Amer., part 4, p. 219. 1869.] (Plate XXXIX, 134.) ..... *L. inornata* O. S.
    Thorax brownish without gray color ..... 19
19. Pleura of thorax grayish, unmarked; size small. [Mon. Dipt. N. Amer., part 4, p. 218. 1869.] ..... *L. contempta* O. S.
    Pleura of thorax dull yellow, with a conspicuous dark brown stripe extending from the cervical sclerites to the postnotum; size larger. [Proc. Acad. Nat. Sci. Phila., p. 592, pl. 25, fig. 3. 1914.] (Plate XXXIX, 136.) ..... *L. nigripleura* A. & L.
    (In the writer's key to the species of the *luteipennis* group [Proc. Acad. Nat. Sci. Phila., p. 593, 1914], in couplet 4 *L. contempta* is given as being a larger species than *L. nigripleura*. This is erroneous, *L. contempta* being the smallest species of the group. It is more southern in its distribution than *L. nigripleura*.)
20. Wings narrow, grayish; stigma distinct, hairy; antennae of male elongated. [*Limnobia tenuipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21. 1823.] (Plate XXXVIII, 121.) ..... *L. tenuipes* (Say)
    Wings broader, more yellowish brown; stigma not distinct; antennae of male short ..... 21
21. Body opaque; front gray. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 122.) ..... *L. imbecilla* O. S.
    Body shiny reddish yellow; front yellowish red. [Mon. Dipt. N. Amer., part 4, p. 212. 1869.] (Plate XXXVIII, 123.) ..... *L. recondita* O. S.
22. Very large species, wing over 18 mm. (Subgenus *Eutonia* v. d. W.) ..... 23
    Smaller species, wing under 15 mm. ..... 24

23. Large, wing of female 21.5 mm.; thoracic dorsum reddish brown with three velvety-brown stripes, the middle one narrowly split by a line of the ground color; ground color of wings yellowish and brown; basal abdominal tergites yellow without prominent setigerous punctures; cross-vein *r* close to the tip of $R_1$. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 126–127, pl. 16, fig. 18. 1909.] (Plate XXXIX, 140.)... *L. alleni* Johns.

Smaller, wing of female 20 mm.; thoracic dorsum gray with three narrow velvety-brown stripes, the middle one split by a broad pale line; ground color of wings hyaline; basal abdominal tergites gray with prominent setigerous punctures; cross-vein *r* more distant from the tip of $R_1$. [Journ. N. Y. Ent. Soc., vol. 24, p. 118–120, pl. 8, fig. 2. 1916.] (Plate XXXIX, 141.)..... *L. marchandi* Alex.

24. $R_{2+3}$ very elongated, nearly twice the length of $R_2$ alone; cross-vein *r* on $R_{2+3}$. [Proc. Acad. Nat. Sci. Phila., p. 238, pl. 4, fig. 26. 1859.] (Plate XXXVIII, 127.) *L. ultima* O. S.

(*L. ultima* is included in both sections of couplet 12 because the character of the position of the cross-vein *r* is slightly variable and there is a possibility of misinterpretation.)

$R_{2+3}$ shorter, not longer than $R_2$ alone; cross-vein *r* on $R_2$.....25

25. Basal deflection of $Cu_1$ at the inner end of cell *1st* $M_2$. (Subgenus *Dactylolabis* O. S.)..26

Basal deflection of $Cu_1$ near the middle of cell *1st* $M_2$.....27

26. Wings spotted with brown. [Proc. Acad. Nat. Sci. Phila., p. 240, pl. 3, figs. 28, 28a. 1859.] (Plate XL, 148.)..... *L. montana* O. S.

Wings unspotted. [Mon. Dipt. N. Amer., part 4, p. 229. 1869.] (Plate XL, 147.) *L. cubitalis* O. S.

27. Wings spotted with brown or distinctly seamed along the cross-veins and deflections of veins.....28

Wings clear, or with only the stigmal spot (in *L. poetica* with a tiny cloud at the origin of *Rs* and the basal deflection of $R_{4+5}$).....35

28. Wings heavily irrorate with brown over the entire surface. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 127–128, pl. 16, fig. 17. 1909.] (Plate XXXIX, 133.)....*L. irrorata* Johns.

Wings not heavily irrorate over the entire surface, the markings appearing as broad seams to the veins or as dark tips to the wings.....29

29. $R_{2+3}$ short or very short, much less than $R_2$ alone; cross-vein *r* at about midlength of $R_2$; petiole of cell $M_1$ longer than or subequal to this cell; brown seams to the veins more extensive; antennae of male short.....30

$R_{2+3}$ very long, subequal to $R_2$ alone; cross-vein *r* just beyond the fork of $R_{2+3}$; petiole of cell $M_1$ distinctly shorter than this cell; brown seams on the wings limited to *r-m* and the deflection of $R_{4+5}$; antennae of male elongated. [Mon. Dipt. N. Amer., part 4, p. 205. 1869.] (Plate XXXVIII, 114.).....*L. unica* O. S.

30. Radial sector short, arcuated to almost square at its origin; cross-vein *r* situated at about midlength of vein $R_2$, which is oblique; outer end of cell $R_2$ very broad due to the oblique nature of vein $R_2$; species with the cross-veins seamed with brown have the tip of the wings more or less infuscated. (Subgenus *Phylidorea* Bigot.).....31

Radial sector longer; vein $R_2$ not oblique and the cell $R_2$ not strikingly broadened at its apex; broad grayish brown seams to the cross-veins, deflections of veins, and along *Cu*, but the wing apex only slightly darkened if at all.....33

31. Coloration of the body yellowish or reddish, the thoracic notum light yellow. [Proc. Acad. Nat. Sci. Phila., p. 235. 1859.] (Plate XXXIX, 128.).....*L. adusta* O. S.

Coloration of the body dark brown to almost black, the thoracic notum concolorous.....32

32. Legs yellow with the brown apices to the segments narrow; costal cell of the wing yellow. [Psyche, vol. 18, p. 195–196, pl. 16, figs. 4, 8. 1911.] (Plate XXXIX, 129.) *L. similis* Alex.

Legs with the femora brown, only a little brightened basally; costal cell of the wings brown. [Journ. N. Y. Ent. Soc., vol. 24, p. 123, pl. 8, fig. 7. 1916.] (Plate XXXIX, 130.)..... *L. terrae-novae* Alex.

33. Large species, wing of male over 9 mm.; male with the pleural appendage of the hypopygium pectinated. (Subgenus *Prionolabis* O. S.) ..... 34
Smaller species, wing of male under 8.5 mm.; male with the pleural appendage of the hypopygium not pectinated, rather sharply pointed. [Journ. N. Y. Ent. Soc., vol. 24, p. 121–122, pl. 8, fig. 5. 1916.] (Plate XL, 146.) ..... *L. terebrans* Alex.

34. Large, wing of male about 13 mm.; costal and subcostal cells of the wings rich yellow; stigma dark brown; bases of femora bright yellow; anterior apical appendage of male hypopygium bifurcate. [Proc. Acad. Nat. Sci. Phila., p. 239, pl. 4, figs. 27, 27a, 27b. 1859.] (Plate XL, 142.) ..... *L. rufibasis* O. S.
Smaller, wing of male about 11.5 mm.; wings uniform light yellowish gray; stigma rather indistinct, grayish; bases of femora brownish yellow; anterior apical appendage of male hypopygium simple. [Psyche, vol. 18, p. 198–199, pl. 16, fig. 10. 1911.] (Plate XL, 143.) ..... *L. simplex* Alex.

35. *Rs* elongated and spurred at its origin; antennae of male elongated. [Mon. Dipt. N. Amer., part 4, p. 207. 1869.] (Plate XXXVIII, 116.) ..... *L. poetica* O. S.
*Rs* usually shorter, if elongated not spurred at origin; antennae of male short except in *L. laricicola* ..... 36

36. $R_{2+3}$ elongated, more or less arcuated, longer than the basal deflection of $Cu_1$ ..... 37
$R_{2+3}$ not conspicuously arcuated, short, little if any longer than the basal deflection of $Cu_1$ ..... 38

37. *Rs* and $R_{2+3}$ strongly arcuated; cell *1st* $M_2$ very broad; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 236. 1859.] (Plate XXXVIII, 126.) ..... *L. toxoneura* O. S.
*Rs* almost straight; $R_{2+3}$ feebly arcuated but elongate; cell *1st* $M_2$ narrow; antennae of male elongated. [Psyche, vol. 19, p. 167, pl. 13, fig. 4. 1912.] (Plate XXXVIII, 120.) ..... *L. laricicola* Alex.

38. Coloration gray; wings with the base strongly yellow, this including *Sc* for its entire length; hind legs with the apical third of femora dark brown, fore femora with the apical two-thirds dark brown; *Rs* rather elongate and somewhat angulated at its origin. [*Phylidorea subcostata* Alex. Can. Ent., vol. 43, p. 288–289. 1911.] (Plate XL, 149.) ..... *L. subcostata* (Alex.)
Coloration not gray; wings with the base not strongly yellow; legs with the femora yellow, the tips narrowly brown ..... 39

39. Coloration yellowish brown; tuberculate pits distinct; *Rs* nearly straight; antennae of male moniliform. [Mon. Dipt. N. Amer., part 4, p. 220. 1869.] ..... *L. fratria* O. S.
Coloration yellow to reddish yellow; tuberculate pits not evident; *Rs* short, strongly arcuated; antennae of male not moniliform. (Subgenus *Phylidorea* Bigot.) ..... 40

40. Large species, wing of male 9.5 mm.; abdomen of male without a black subterminal annulus. [Journ. N. Y. Ent. Soc., vol. 8, p. 191. 1900.] (Plate XXXIX, 132.) *L. lutea* Doane
Smaller species, wing of male less than 7.5 mm.; abdomen of male with a black subterminal annulus. [Proc. Acad. Nat. Sci. Phila., p. 594, pl. 25, fig. 4. 1914.] (Plate XXXIX, 131.) ..... *L. novae-angliae* Alex.

41. Cell $R_2$ of the wings broadly sessile. [Proc. Acad. Nat. Sci. Phila., p. 597, pl. 27, fig. 28. 1914.] (Plate XL, 151.) ..... *L. emmelina* Alex.
Cell $R_2$ of the wings petiolate ..... 42

42. Bases of cells $R_3$ and *1st* $M_2$ conspicuously nearer the wing root than cell $R_5$; petiole of cell $R_2$ less than half the length of vein $R_2$; vein $R_2$ not short, oblique; veins issuing from cell *1st* $M_2$ about twice the length of the cell ..... 43
Bases of cells $R_3$, $R_5$, and *1st* $M_2$ about on a level; petiole of cell $R_2$ more than half the length of vein $R_2$; vein $R_2$ short, oblique; veins issuing from cell *1st* $M_2$ about equal to or a little longer than the cell, if longer (as in *L. edwardi*) not twice this length ..... 44

43. Prescutal stripes not well-defined; tuberculate pits present; *r* far removed from the tip of $R_1$; basal deflection of $Cu_1$ usually at from one-third to one-half the length of the cell *1st* $M_2$. (Subgenus *Pseudolimnophila* Alex.) [Psyche, vol. 18, p. 196–198, pl. 16, fig. 3. 1911.] (Plate XL, 150.) ..... *L. noveboracensis* Alex.

Prescutal stripes dark brown; tuberculate pits lacking; $r$ at the tip of $R_1$; basal deflection of $Cu_1$ usually at or close to the fork of $M_1$. [Proc. Acad. Nat. Sci. Phila., p. 534–535, pl. 27, fig. 46. 1916.] (Plate XL, 157.) ..... *L. sylvia* Alex.

44. $Rs$ short, about equal to vein $R_2$ of the wings. [Proc. Acad. Nat. Sci. Phila., p. 241. 1859.] (Plate XL, 152.) ..... *L. lenta* O. S.

$Rs$ elongate, equal to about twice the length of vein $R_2$ of the wings ..... 45

45. Mesonotum and pleura yellowish or brownish yellow; wings pale yellow. [Proc. Acad. Nat. Sci. Phila., p. 595–596, pl. 25, fig. 5. 1914.] (Plate XL, 155.) *L. stanwoodae* Alex.

Mesonotum and pleura not yellow ..... 46

46. Pleura and mesonotum clear bluish black with a gray bloom, only the coxae conspicuously light yellow; wings with a yellowish tinge; cross-vein $r$ beyond the fork of $R_{2+3}$ on $R_2$. [Proc. Acad. Nat. Sci. Phila., p. 241. 1859.] (Plate XL, 153.) ..... *L. quadrata* O. S.

Pleura and mesonotum not so colored; cross-vein $r$ at or before the fork of $R_{2+3}$ ..... 47

47. Pleura of thorax with a conspicuous black dorsal stripe; mesonotum rich brown; wings with a brown suffusion; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 596, pl. 25, fig. 6. 1914.] (Plate XL, 154.) ..... *L. osborni* Alex.

Pleura of thorax without a black dorsal stripe; mesonotum dull yellowish with three confluent dark brown stripes; wings without a distinct dark brown suffusion; antennae of male elongated. [Proc. Acad. Nat. Sci. Phila., p. 533–534, pl. 27, fig. 45. 1916.] (Plate XL, 156) ..... *L. edwardi* Alex.

## Tribe **Hexatomini**

The genera of the tribe Hexatomini may be separated in accordance with the following key:

1. Cell *1st* $M_2$ open; but one free branch of the media reaching the wing margin; cell $R_2$ tiny ..... *Hexatoma* Latr. (p. 920)

Cell *1st* $M_2$ closed; two or three free branches of the media reaching the wing margin; cell $R_2$ larger, more elongate ..... 2

2. Feet (in the local species) white; stigma small; cell $M_1$ present. *Penthoptera* Schin. (p. 921)

Feet not white; stigma large; cell $M_1$ present or absent ..... *Eriocera* Macq. (p. 921)

### Genus **Hexatoma** Latreille

1809 *Hexatoma* Latr. Gen. Crust. et Ins., vol. 4, p. 260.
1818 *Anisomera* Meig. Syst. Beschr., vol. 1, p. 210.
1818 *Nematocera* Meig. Syst. Beschr., vol. 1, p. 209.
1836 *Peronecera* Curt. Brit. Ent., p. 589.

The small genus Hexatoma includes seventeen described species, about all of which are European. They are mostly small species, with a reduced medial venation that is at first sight difficult to interpret; the manner in which this genus has been evolved from Eriocera is well shown in some of the plastic species of the latter genus, notably *E. austera* Doane, in which all gradations in venation between Eriocera and Hexatoma may be found in a small series. From species such as these it is seen that the elimination of the posterior branch of the media is brought about by

fusion rather than by atrophy. The larvae are carnivorous, and live in wet sand and gravel along the margins of streams (Alexander, 1915 a: 141–148).

*Hexatoma megacera* (O. S.)

1859 *Anisomera megacera* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1909 *Hexatoma megacera* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 126.

*Hexatoma megacera* is a small, blackish gray fly, the mesonotum having three darker stripes and the male antennae being somewhat elongated and filiform. The characteristic venation is shown in Plate XXXVII, 112.

Genus **Penthoptera** Schiner

1863 *Penthoptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 220.

In the genus Penthoptera there are seven species — four from Europe, two from tropical America, and one local species. The immature stages are spent in rich organic earth, a very different habitat from that of the larvae of the related genera Eriocera and Hexatoma. The larva is carnivorous (Alexander, 1915 a: 152–157). In the native species, *Penthoptera albitarsis*, the feet are pure snowy white, which makes the insect a conspicuous one.

*Penthoptera albitarsis* O. S.

1869 *Penthoptera albitarsis* O. S. Mon. Dipt. N. Amer., part 4, p. 257.

*Penthoptera albitarsis* is a brownish fly, with the thorax bluish gray, the wings slightly tinged with dusky, and the feet pure snowy white. The flies occur in cool, shady situations and are often very common. In the South (North Carolina) they are frequent in gum swamps. The venation is shown in Plate XXXVII, 104.

Genus **Eriocera** Macquart

1830 *Caloptera* Guer. Voyage de la Coquille, Zool., Ins., pl. 20, fig. 2.
1838 *Eriocera* Macq. Dipt. Exot., vol. 1, p. 74.
1838 *Evanioptera* Guer. Voyage de la Coquille, Zool., vol. 2, p. 287.
1848 *Pterocosmus* Walk. List Dipt. Brit. Mus., vol. 1, p. 78.
1850 *Allarithmia* Loew. Bernstein und Bernsteinfauna, p. 38.
1857 *Oligomera* Dolesch. Natuurk. Tijdschr. Nederl. Indie, vol. 14, p. 387.
1859 *Arrhenica* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1859 *Physecrania* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 7, p. 123.
1912 *Androclosma* Enderlein. Zool. Jahrb., vol. 32, part 1, p. 34.
1916 *Globericera* Matsumura. Thous. Ins. Japan, add. 2, p. 471.

Eriocera is one of the larger genera of crane-flies, including about one hundred described species which are most numerous in the tropics of both hemispheres. The larvae are carnivorous. They live in streams, and pupate in sand or gravel (Alexander and Lloyd, 1914). The habits of the common local species *E. longicornis* have been described by the author in another paper (Alexander, 1915 a:149–152). The following key divides the local species of Eriocera:

1. Cell $M_1$ present ..... 2
   Cell $M_1$ lacking ..... 3
2. Antennae of male greatly elongated, more than twice the length of the whole body; wings grayish brown; vertical tubercle prominent, brownish on the sides. [*Arrhenica spinosa* O. S. Proc. Acad. Nat. Sci. Phila., p. 244, pl. 4, fig. 30. 1859.] (Plate XXXVII, 105.) ..... *E. spinosa* (O. S.)
   Antennae short in both sexes, extending about to the wing root or a little beyond; wings darker brown; vertical tubercle low, grayish. [Bul. U. S. Geol. Survey, vol. 3, p. 205. 1877.] (Plate XXXVII, 106.) ..... *E. brachycera* O. S.
3. Color of body yellow or yellowish red ..... 4
   Color of body brown, gray, or black ..... 5
4. Antennae of male elongated, longer than the body; a blackish spot on the scutal lobes above the wing root. [Mon. Dipt. N. Amer., part 4, p. 255. 1869.] (Plate XXXVII, 109.) ..... *E. wilsonii* O. S.
   (*E. antennaria* Doane [Journ. N. Y. Ent. Soc., vol. 8, p. 194, pl. 8, fig. 12, 1900] is the same as *E. wilsonii* O. S.)
   Antennae short in both sexes; no blackish spot on the scutal lobes above the wing root. [Journ. N. Y. Ent. Soc., vol. 8, p. 194, pl. 8, fig. 13. 1900.] ..... *E. aurata* Doane
5. Thoracic dorsum gray; antennae of male elongated ..... 6
   Thoracic dorsum brown or black; antennae short in both sexes ..... 7
6. Vertical tubercle of male very large and high, greater than length of eye; first segment of antennal scape uniformly dark; prescutal stripes broad, dark brown, the median stripes about confluent and continued cephalad to the pronotum; cell *1st* $M_2$ of wings short, pentagonal, usually with a spur into cell $R$; valves of ovipositor short, blunt, sub-fleshy. [*Anisomera longicornis* Walk., List Dipt. Brit. Mus., vol. 1, p. 82. 1848.] (Plate XXXVII, 107.) ..... *E. longicornis* (Walk.)
   (*E. gibbosa* Doane [Journ. N. Y. Ent. Soc., vol. 8, p. 193, pl. 8, fig. 10, 1900] is a doubtful species; in its coloration and, especially, in its venation, it is strikingly like *E. longicornis* [Walk.], but there is no mention in the original description of the size of the antennae.)
   Vertical tubercle of male moderate in size, not so high as length of eye; first segment of antennal scape pale beneath; prescutal stripes narrow, pale brown, the two middle stripes separate, becoming obliterated at about the level of the tuberculate pits; cell *1st* $M_2$ of wings long, hexagonal; valves of ovipositor elongated, pointed, chitinized. [Psyche, vol. 19, p. 169–170, pl. 13, fig. 9. 1912.] (Plate XXXVII, 108.) ..... *E. cinerea* Alex.
7. Cell $R_2$ short, cross-vein $r$ inserted on $R_{2+3}$. [Psyche, vol. 19, p. 168–169, pl. 13, fig. 7. 1912.] (Plate XXXVII, 111.) ..... *E. fultonensis* Alex.
   Cell $R_2$ deep, cross-vein $r$ inserted on $R_2$ ..... 8
8. Wings brown, the stigma small, rounded, brown; abdominal tergites brown. [Proc. Acad. Nat. Sci. Phila., p. 243, pl. 3, fig. 31. 1859.] ..... *E. fuliginosa* O. S.
   Wings blackish brown, the stigma oval, dark brown; abdominal tergites black. [Proc. Acad. Nat. Sci. Phila., p. 602. 1914.] (Plate XXXVII, 110.) ..... *E. tristis* Alex.

*Eriocera longicornis*, *E. cinerea*, and *E. spinosa* are on the wing in late April and May, the last-named species flying in July. *E. brachycera*, *E. fultonensis*, *E. fuliginosa*, and *E. tristis* are on the wing during the summer months.

## Tribe Pediciini

The genera of the tribe Pediciini may be separated in accordance with the following key:

1. Antennae with 16 segments ..... 2
   Antennae with 13 or 15 segments ..... 3
2. Cord oblique; cell *1st* $M_2$ very short, pentagonal; size large, wing over 20 mm.; palpi elongated ..... *Pedicia* Latr. (p. 923)
   Cord transverse; cell *1st* $M_2$ elongate; size smaller, wing under 18 mm.; palpi short. *Tricyphona* Zett. (p. 924)
3. A supernumerary cross-vein in cell $R_1$ ..... *Dicranota* Zett. (p. 925)
   No supernumerary cross-vein in cell $R_1$. (Genus *Rhaphidolabis* O. S.) ..... 4
4. Cell $M_1$ absent ..... Subgenus *Plectromyia* O. S. (p. 925)
   Cell $M_1$ present ..... 5
5. Antennae 15-segmented; cell *1st* $M_2$ closed ..... Subgenus *Rhaphidolabina* Alex. (p. 925)
   Antennae 13-segmented; cell *1st* $M_2$ open ..... Subgenus *Rhaphidolabis* O. S. (p. 925)

The recent accession of several curious new venational types in this tribe indicates that the vein herein held to be the radial cross-vein is in reality the upward deflection of $R_2$, which, in most species, is short and transverse or but slightly oblique and is fused distally with $R_1$. A detailed account of this venational peculiarity may be consulted elsewhere (Alexander, 1918 d).

### Genus **Pedicia** Latreille

1809 *Pedicia* Latr. Gen. Crust. et Ins., vol. 4, p. 255.
1916 *Daimiotipula* Matsumura. Thous. Ins. Japan, add. 2, p. 463.

Pedicia is a small genus including six species, four of which are North American. The species are among the largest of the Limnobiinae, and with their conspicuous brown-and-white wings attract considerable attention. The larvae are carnivorous, living beneath moss in percolating water and in cold springs (Needham, 1903 b:285–286). There are two regional species, both of which were originally described from Nova Scotia by Walker. The following key divides the local species of Pedicia:

Wings with the costal margin brown; vein $Cu_2$ seamed with dark brown. [List Dipt. Brit. Mus., vol. 1, p. 37. 1848.] (Plate XLII, 175.) ..... *P. albivitta* Walk.
Wings with the costal margin brownish yellow; no brown seam on vein $Cu_2$. [List Dipt. Brit. Mus., vol. 1, p. 38. 1848.] (Plate XLII, 176.) ..... *P. contermina* Walk.

## Genus **Tricyphona** Zetterstedt

1838 *Tricyphona* Zett. Ins. Lapponica, Dipt., p. 851.
1856 *Amalopis* Hal. Ins. Brit., Dipt., vol. 3, add., p. xv.
1860 *Crunobia* Kol. Wien. Ent. Monatschr., vol. 4, p. 391.
1869 *Amalopis* O. S. Mon. Dipt. N. Amer., part 4, p. 260.

There are about forty known species in the genus Tricyphona. Almost all of these are Holarctic in their distribution, but two occur in the Australasian region. The carnivorous larvae live in moist earth. The following key divides the local species:

1. Cell *M* with a supernumerary cross-vein; wings heavily clouded and marbled with gray. [*Amalopis hyperborea* O. S. Proc. Acad. Nat. Sci. Phila., p. 292. 1861.] (Plate XLII, 182.) ..... *T. hyperborea* (O. S.)
   Cell *M* without a supernumerary cross-vein; wings with the markings sparse, confined to the region of the veins ..... 2
2. Cell $R_2$ short-petiolate; costal margin of wings infuscated. [*Amalopis inconstans* O. S. Proc. Acad. Nat. Sci. Phila., p. 247, pl. 3, fig. 32. 1859.] (Plate XLII, 177.) *T. inconstans* (O. S.)
   Cell $R_2$ sessile; costal margin of wings not infuscated ..... 3
3. Wings subhyaline or hyaline, unspotted ..... 4
   Wings spotted or marked with darker ..... 5
4. Stigma of wings brown; male hypopygium conspicuously hairy; wings of female subatrophied. [Can. Ent., vol. 49, p. 30–31. 1917.] (Plate XLII, 179, 180.) *T. autumnalis* Alex.
   Stigma of wings pale; male hypopygium small, not conspicuously hairy; wings of female normally developed. [*Amalopis calcar* O. S. Proc. Acad. Nat. Sci. Phila., p. 247. 1859.] (Plate XLII, 178.) ..... *T. calcar* (O. S.)
5. Fusion of $Cu_1$ with $M_3$ extensive, subequal to the part of $M_3$ before the cross-vein *m*. [*Amalopis auripennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 247. 1859.] (Plate XLII, 181.) ..... *T. auripennis* (O. S.).
   Fusion of $Cu_1$ with $M_3$ transient if present at all, usually less than one-half of the part of $M_3$ before the cross-vein *m* ..... 6
6. Coloration of body light brown; *m-cu* obliterated by the fusion of $Cu_1$ on $M_3$. [Proc. Acad. Nat. Sci. Phila., p. 598–599, plate, fig. 1914.] (Plate XLII, 183.) *T. katahdin* Alex.
   Coloration of body gray; *m-cu* present ..... 7
7. Scape of antenna yellowish or brownish yellow, the flagellum much darker, brown; abdominal tergites brown, the margins of the segments pale producing a banded appearance; wings with large rounded clouds at the tips of the longitudinal veins and along the cross-veins. [*Amalopis vernalis* O. S. Proc. Acad. Nat. Sci. Phila., p. 291. 1861.] (Plate XLII, 185.) ..... *T. vernalis* (O. S.)
   Scape of antenna dark brown, concolorous with the flagellum; abdominal tergites brown, unbanded; wings with the pattern almost obsolete, reduced to tiny dots and seams. [Proc. Acad. Nat. Sci. Phila., p. 538–540 pl. 28, fig. 53. 1916.] (Plate XLII, 184.) *T. paludicola* Alex.

In the local fauna, *T. vernalis* and *T. paludicola* are early spring species, *T. auripennis* and *T. calcar* late spring species, and *T. katahdin* and *T. autumnalis* late summer species.

## Genus **Dicranota** Zetterstedt

1838 *Dicranota* Zett. Ins. Lapponica, Dipt., p. 851.

In the genus Dicranota there are about fifteen known species, restricted to the northern Holarctic region. The species are readily distinguished from those of Rhaphidolabis by the supernumerary cross-vein in cell $R_1$ of the wings. The larvae are carnivorous, feeding largely on Tubifex worms (Miall, 1893). The local species of Dicranota may be separated according to the following key, which is adapted from a key to the North American species already published by the author (Alexander, 1914 b:601).

1. Cell $M_1$ absent ..... 2
   Cell $M_1$ present ..... 3
2. Halteres with the knobs darkened; antennae of male much longer than the thorax. [Mon. Dipt. N. Amer., part 4, p. 281–282. 1869.] ..... *D. eucera* O. S.
   Halteres pale; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 249. 1859.] (Plate XLI, 169.) ..... *D. rivularis* O. S.
3. Cell *1st* $M_2$ present; color of body yellowish. [Proc. Acad. Nat. Sci. Phila., p. 599–600, pl. 27, fig. 31. 1914.] (Plate XLI, 167.) ..... *D. pallida* Alex.
   Cell *1st* $M_2$ absent; color of body gray. [Proc. Acad. Nat. Sci. Phila., p. 600. 1914.] (Plate XLI, 168.) ..... *D. noveboracensis* Alex.

## Genus **Rhaphidolabis** Osten Sacken

1869 *Rhaphidolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 284.
1869 *Plectromyia* O. S. Mon. Dipt. N. Amer., part 4, p. 282.

The genus Rhaphidolabis includes about fourteen described species found in the Holarctic region and in the mountainous sections of the Oriental region. The larvae are carnivorous, and live in rich organic mud or in the streams near by. Needham (1908:212–214) has given a description of the larva of the species *R. tenuipes*. The following key, adapted from a key to the North American species of Rhaphidolabis already published by the author (Alexander, 1916:541–542), divides the local species of the genus:

1. Antennae 15-segmented; cross-vein *m* present. (Subgenus *Rhaphidolabina* Alex.) [Mon. Dipt. N. Amer., part 4, p. 288. 1869.] (Plate XLI, 170.) ..... *R. flavcola* O. S.
   Antennae 13-segmented; cross-vein *m* absent ..... 2
2. Cell $M_1$ absent. (Subgenus *Plectromyia* O. S.) [*Plectromyia modesta* O. S. Mon. Dipt. N. Amer., p. 284. 1869.] (Plate XLI, 174.) ..... *R. modesta* (O. S.)
   Cell $M_1$ present. (Subgenus *Rhaphidolabis* O. S.) ..... 3
3. Cell $R_2$ petiolate. [Mon. Dipt. N. Amer., p. 287. 1869.] (Plate XLI, 171.) *R. tenuipes* O. S.
   Cell $R_2$ sessile ..... 4

4. Coloration grayish brown, the prescutum with three dark brown stripes; abdomen dark brown with paler caudal margins to the segments; wings very pale brown, the radial sector very short, arcuated, angulated, or spurred. [Proc. Acad. Nat. Sci. Phila., p. 543–544, pl. 28, fig. 57. 1916.] (Plate XLI, 173.) ..... *R. cayuga* Alex.
Coloration reddish brown, the prescutum with three indistinct stripes; abdomen yellowish brown, the hypopygium bright yellow; wings nearly hyaline, the radial sector somewhat elongated, slightly arcuated. [Proc. Acad. Nat. Sci. Phila., p. 544–545, pl. 28, fig. 58. 1916.] (Plate XLI, 172.) ..... *R. rubescens* Alex.

## SUBFAMILY **Cylindrotominae**

The genera of the subfamily Cylindrotominae may be separated in accordance with the following key:

1. Head and intervals of the prescutum with numerous deep punctures.
*Triogma* Schin. (p. 926)
Head and intervals of the prescutum smooth ..... 2
2. Three branches of the radius reaching the wing margin.
*Phalacrocera* Schin. (species *neoxena* Alex.) (p. 927)
Two branches of the radius reaching the wing margin, caused by an apparent fusion of $R_{1+2+3}$ ..... 3
3. Three branches of the media reaching the wing margin .... *Cylindrotoma* Macq. (p. 927)
Two branches of the media reaching the wing margin ..... 4
4. Cross-vein *r-m* present; cross-vein *m* obliterated by the fusion of $M_3$ on $M_{1+2}$; antennae of male tipuline in structure ..... *Phalacrocera* Schin. (species *tipulina* O. S.) (p. 927)
Cross-vein *r-m* usually obliterated by the fusion of $R_{4+5}$ on $M_{1+2}$; cross-vein *m* present; antennae of male subpectinate, the individual flagellar segments almost cordate.
*Liogma* O. S. (p. 927)

### Genus **Triogma** Schiner

1863 *Triogma* Schin. Wien. Ent. Monatschr., vol. 7, p. 223.

There are but two known species of Triogma, one occurring in Europe and the other in northeastern North America. The larval life of the European species, the only one that is known, is spent on aquatic mosses growing in mountain torrents. The insects closely resemble the species of Liogma in all their stages.

### *Triogma exculpta* O. S.

1865 *Triogma exculpta* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.

*Triogma exculpta* is a rather small, dull brown fly, with the wings suffused with brown. The head and the sides of the thorax are deeply punctured. The fly is rare and is insufficiently known. The venation is very much like that in the genus Liogma. (Johnson, 1909:131.)

## Genus **Phalacrocera** Schiner

1863 *Phalacrocera* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

The small genus Phalacrocera includes but three described species—two North American and one European. They are of especial interest because of certain venational features which they possess and which aid materially in explaining the remarkable venation of the more specialized species of Cylindrotominae (p. 863). The larva is aquatic, living on submerged plants. It is greenish brown in color, and the body is provided with numerous long, flexible filaments which are quite unlike the spiny armature of the more specialized members of the subfamily. The species are northern in their distribution and are most frequently found in bogs and boggy meadows. The local species may be separated by the following key:

Vein $R_2$ present and persistent to the wing margin; wings dark brown. [Proc. Acad. Nat. Sci. Phila., p. 603–605, pl. 25, fig. 10. 1914.] (Plate XXX, 9.) ... *P. neoxena* Alex.

Vein $R_2$ lost by atrophy; wings grayish brown. [Proc. Ent. Soc. Phila., vol. 4, p. 241. 1865.] (Plate XXX, 8.) ..... *P. tipulina* O. S.

## Genus **Cylindrotoma** Macquart

1834 *Cylindrotoma* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 107.

The genus Cylindrotoma forms a small group of crane-flies, including two European and three North American species. They are all similar in color, being usually bright yellow with black stripes on the thorax, in this respect suggesting some species of Nephrotoma. The larvae live on the lower side of the leaves of various monocotyledonous and dicotyledonous plants such as Allium, Anemone, Trautvetteria, Stellaria, and Viola, the insect feeding on the leaf tissue. The larvae are green in color and are usually provided with fleshy points and processes.

The following key divides the local species of Cylindrotoma:

Tarsi dark brown. [Proc. Ent. Soc. Phila., vol. 4, p. 236. 1865.] (Plate XXX, 6.) *C. americana* O. S.

Tarsi yellow. [*C. tarsalis* Johns., Psyche, vol. 19, p. 2, fig. 4, 1912. *C. anomala* Johns., Psyche, vol. 19, p. 2–3, fig. 3, 1912.] (Plate XXX, 7.) ..... *C. tarsalis* Johns.

## Genus **Liogma** Osten Sacken

1869 *Liogma* O. S. Mon. Dipt. N. Amer., part 4, p. 298.

In the genus Liogma there are three described species, all occurring in the North Temperate Zone. The coloration of the adult flies is

sordidly yellow and black, with the surface shiny. The antennae of the male are submoniliform with the segments heart-shaped, as shown in figure 125, 1 (page 850). The larva, which has been discussed by the writer in another paper (Alexander, 1914 a), lives in certain terrestrial mosses (as Hypnum). It is bright green in color, with darker stripes on the sides, and closely simulates the appearance of its host plant, the illusion being heightened by the spines and excrescences that cover the body.

*Liogma nodicornis* (O. S.)

1865 *Triogma nodicornis* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.
1887 *Liogma nodicornis* O. S. Berl. Ent. Ztschr., vol. 31, p. 226.

*Liogma nodicornis* is a common fly in Canadian conditions thruout North America. In color it is mainly yellow, the head black and shiny, the thorax yellow with three more or less confluent shiny black stripes on the dorsum, the pleura with one or two large black blotches. The venation (Plate XXX, 5) is somewhat variable, especially in the fusion of $R_{4+5}$ on $M_{1+2}$, these being in some cases broadly fused (as shown in figure 128, 1, page 862), in other cases with the cross-vein *r-m* apparent.

## SUBFAMILY **Tipulinae**

### Tribe **Dolichopezini**

The genera of the tribe Dolichopezini may be separated in accordance with the following key:

1. Tip of vein $R_2$ atrophied; *Rs* very short, transverse, simulating a cross-vein; second anal vein long, about two-thirds the length of the first; *Sc* moderate in length, ending in *R* ..... 2
   Tip of vein $R_2$ present, the vein almost perpendicular to $R_{2+3}$ at its origin; *Rs* long, strongly arcuated at its origin; second anal vein very short, about one-third the length of the first; *Sc* very long, ending in costa ..... *Brachypremna* O. S. (p. 928)
2. Cell *1st* $M_2$ lacking; basal deflection of $Cu_1$ in a long fusion with *M*, breaking away before the fork of *M* ..... *Dolichopeza* Curt. (p. 929)
   Cell *1st* $M_2$ present; basal deflection of $Cu_1$ in punctiform contact with $M_{3+4}$ beyond the fork of *M* ..... *Oropeza* Needm. (p. 929)

### Genus **Brachypremna** Osten Sacken

1886 *Brachypremna* O. S. Berl. Ent. Ztschr., vol. 30, p. 161.

The genus Brachypremna includes but seven described species, all of which are tropical American. A single species, *B. dispellens*, ranges

into the southern limits of the territory here considered. This is a curious fly which is common all over the South, where in some sections it is called "weaver." The flies of this species have a remarkable dance over a vertical height of several feet, and have been aptly termed "the kings of the dancing crane-flies." The larval life is spent in decaying wood.

*Brachypremna dispellens* (Walk.)

1860 *Tipula dispellens* Walk. Trans. Ent. Soc. Lond., n. ser., vol. 5, p. 334.
1886 *Brachypremna dispellens* O. S. Berl. Ent. Ztschr., vol. 30, p. 152.

*Brachypremna dispellens* is a large, brownish fly. The pleura is silvery white with narrow brown stripes. The legs are very long, and the tibiae and tarsi are pale yellowish white. The venation is shown in Plate XLIII, 188.

Genus **Dolichopeza** Curtis

1825 *Dolichopeza* Curt. Brit. Ent., p. 62.
1830 *Leptina* Meig. Syst. Beschr., vol. 6, pl. 65, fig. 10.
1846 *Apeilesis* Macq. Dipt. Exot., Suppl. 1, p. 8.

The genus Dolichopeza includes about eighteen described species, only one of which occurs in the New World. The immature stages are spent in or beneath moist mosses.

*Dolichopeza americana* Needm.

1908 *Dolichopeza americana* Needm. 23d Rept. N. Y. State Ent., p. 211, pl. 16, fig. 5.

*Dolichopeza americana* is a curious fly usually found beneath bridges and culverts, or in similar darkened situations. The adults hang suspended from the roof by the anterior two pairs of feet, the wings being spread wide apart and the long, white-tipped hind legs dangling conspicuously. The dark color of the body and the pure white tarsi easily serve to distinguish the species from the forms of Oropeza that may be found with it. The wing venation is shown in Plate XLIII, 187.

Genus **Oropeza** Needham

1908 *Oropeza* Needm. 23d Rept. N. Y. State Ent., p. 211.

In the genus Oropeza there are seven described species, all occurring within the limits of this paper. While they are closely related to one another, most of them are apparently valid species. They occur in the

same type of situations as does the preceding species — beneath bridges, culverts, in crannies of cliffs, on the inclined sides of boulders along mountain streams, and in similar places. Their position when at rest is very different from that of *Dolichopeza americana*, as they hang from the roof by the front pair of feet only, the other legs dangling and the wings being folded over the abdomen. In this last-named feature they differ conspicuously from the often-associated Dolichopeza. The immature stages are spent in moist earth, or (in the case of *O. obscura*) in a dry moss, *Hedwigia albicans*, where they were first discovered by Hyslop. The larvae are sluggish and of a rather dark green color. The following key is adapted from one given by Johnson (1909:117–118):

1. Tarsi, at least, entirely white ..... 2
   Tarsi yellow or brownish ..... 3
2. Digitiform appendages of male genitalia short or rudimentary; ventral margin deeply and narrowly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 121, pl. 15, fig. 12. 1909.] ..... *O. albipes* Johns.
   Digitiform appendages of male genitalia moderate in length; ventral margin broadly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 121–122, pl. 15, figs. 5, 11. 1909.] ..... *O. subalbipes* Johns.
3. Halteres with the knobs dark brown ..... 4
   Halteres entirely yellow ..... 7
4. Stripes of thorax distinct; ventral margin deeply emarginate ..... 5
   Stripes of thorax obscure; ventral margin but slightly emarginate ..... 6
5. Pleura yellow, unspotted. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 119–120, pl. 15, fig. 6. 1909.] ..... *O. dorsalis* Johns.
   Pleura yellow, spotted. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 120, pl. 15, fig. 9. 1909.] ..... *O. venosa* Johns.
6. Thorax opaque. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 122, pl. 15, figs. 7, 10. 1909.] (Plate XLIII, 186.) ..... *O. obscura* Johns.
   Thorax shining. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 122–123, pl. 15, fig. 8. 1909.] ..... *O. obscura polita* Johns.
7. Ventral margin of male genitalia deeply and narrowly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 118–119, pl. 15, figs. 2, 3, 1909. New name for *Tipula annulata* Say, Journ. Acad. Nat. Sci. Phila., vol. 3, p. 25 (1823), preoccupied.] ..... *O. sayi* Johns.
   Ventral margin broadly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 119, pl. 15, fig. 4. 1909.] ..... *O. similis* Johns.

## Tribe **Ctenophorini**

The following key separates the two genera of the tribe Ctenophorini:

Antennae of male with three pectinations on the flagellar segments, each segment with a single pectination on the apical half in addition to the usual basal pair; ovipositor of female greatly elongated, saber-like ..... *Tanyptera* Latr. (p. 931)

Antennae of male with two pairs of pectinations on the flagellar segments, one pair being subbasal and the other subapical; ovipositor of female short and of the normal tipuline structure ..... *Ctenophora* Meig. (p. 931)

## Genus **Tanyptera** Latreille

1805 *Tanyptera* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 286.
1832 *Xiphura* Brulle. Ann. Soc. Ent. France, vol. 1, p. 206.

In the genus Tanyptera there are supposedly twelve described species, of which three or four are from eastern North America and the remainder are from the Palaearctic region. The remarkable variation in color, however, is strongly indicative that the number of species is very much less than that given, and it is possible that there is but a single species within the limits of this paper. The question can be definitely settled only by the wholesale breeding of larvae to the adult stage. Until more is known about these flies it is best to recognize the full number of forms, always keeping in mind, however, the foregoing remarks.

The larvae live in the wood of deciduous trees, often in prostrate trunks that are fairly sound. The adult flies are easily distinguished from all other crane-flies by the tripectinate antennal segments of the male and the elongated acicular ovipositor in the female. The flies are shiny, and often are brilliantly colored with black and reddish yellow, simulating Ichneumonidae and other hymenopterous insects.

The following key divides the local species of Tanyptera:

1. Wings smoky black; body coloration black, the male with feet and abdomen also black, the female with legs and base of abdomen reddish yellow. [*Ctenophora fumipennis* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 47. 1864.] ..... *T. fumipennis* (O. S.)
   Wings not black ..... 2
2. Wings tinged with topazine yellow, the stigma dark brown; body coloration varying from black to yellow, the feet reddish yellow. [*Ctenophora topazina* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 47–48. 1864.] ..... *T. topazina* (O. S.)
   Wings hyaline, the stigma brown; head black; body coloration varying from black to yellow. [*Ctenophora frontalis* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 48–49. 1864.] (Plate XLIII, 191.) ..... *T. frontalis* (O. S.)

## Genus **Ctenophora** Meigen

1800 *Flabellifera* Meig. Nouv. Class. Mouch., p. 13 (*nomen nudum*).
1803 *Ctenophora* Meig. Illiger's Mag., vol. 2, p. 263.
1910 *Phoroctenia* Coq. Proc. U. S. Nat. Mus., vol. 37, p. 589.

In the genus Ctenophora a condition exists which is similar to that in Tanyptera, there being fifteen described species which are very closely related and many of which are undoubtedly synonymous. Two forms are here recognized, and even these may represent but one species. A number of larvae of Ctenophora were found in a decaying tree by Johannsen (1910), who reared from them a considerable number of adults

which showed well the dimorphic nature of the flies of this group. Some of the specimens of each sex were entirely black, while others were reddish yellow with the wings tipped with darker. Specimens having hyaline wings are often taken.

The larvae live in decaying wood. The adult flies are easily distinguished by the double bipectinate antennae of the male (fig. 125, M, page 850), and the serrate antennae and relatively short ovipositor in the female.

The local species of the genus may be separated by the following key:

Wings with the entire apex beyond the cord tinged with blackish; thorax yellowish brown with darker spots. [Proc. Ent. Soc. Phila., vol. 3, p. 45–46. 1864.] (Plate XLIII, 189, normal form; 190, black form, the wing not shaded in this drawing.) ..... *O. apicata* O. S.

Wings nearly hyaline, with a large brown cloud between the cord and the wing tip but not reaching the apex; thorax yellow with a wedge-shaped median brown stripe. [Proc. Ent. Soc. Phila., vol. 3, p. 46. 1864.] ..... *C. nubecula* O. S.

## Tribe **Tipulini**

The genera of the tribe Tipulini may be separated in accordance with the following key:

1. Flagellar segments of antennae not verticillate ..... *Stygeropis* Loew (p. 932)
   Flagellar segments of antennae verticillate ..... 2
2. Abdomen greatly elongated in both sexes, much longer than the wing alone; the male hypopygium simple in structure, the ninth sternite very long with the pleurites lying in this concavity ..... 3
   Abdomen not greatly elongated in the male sex, rarely so in the female sex (*Tipula longiventris*), not longer than the wing; the male hypopygium more complicated in structure, if simple the ninth sternite not shaped as described above ..... 4
3. Cell $M_1$ sessile; wings strongly suffused with reddish brown ..... *Aeshnasoma* Johns. (p. 933)
   Cell $M_1$ petiolate, long-petiolate in *Longurio minimus*, short-petiolate in *L. testaceus*; wings grayish, the subcostal cell brown ..... *Longurio* Loew (p. 933)
4. *Rs* usually very short, almost transverse, simulating a cross-vein; cell $M_1$ sessile or short-petiolate; basal deflection of $Cu_1$ or the *m-cu* cross-vein joining *M* at or before its fork; coloration usually yellow and black, shiny ..... 5
   *Rs* usually longer, not simulating a cross-vein; cell $M_1$ always petiolate; basal deflection of $Cu_1$ or the *m-cu* cross-vein joining *M* at its fork or underneath the middle of cell *1st* $M_2$; coloration usually dull brown, yellow, or gray. (Genus *Tipula* Linn.) ..... 6
5. Cells of wings glabrous ..... *Nephrotoma* Meig. (p. 934)
   Apical cells of wings pubescent ..... Subgenus *Odontotipula* Alex. (p. 943)
6. Cells of wings glabrous ..... Subgenus *Tipula* Linn. (p. 942)
   Apical cells of wings pubescent ..... 7
7. Apical cells of wings with an abundant short pubescence; body coloration dull brown, as in species of Oropeza ..... Subgenus *Trichotipula* Alex. (p. 942)
   Apical cells of wings with a sparse short pubescence; thoracic dorsum dark-colored with paler stripes ..... Subgenus *Cinctotipula* Alex. (p. 943)

### Genus **Stygeropis** Loew

1844 *Prionocera* Loew. Stett. Ent. Ztg., vol. 5, p. 170; preoccupied.
1863 *Stygeropis* Loew. Berl. Ent. Ztschr., vol. 7, p. 298.

The genus Stygeropis includes about ten species, all confined to the temperate and arctic regions. The species of Stygeropis are readily distinguished from those of Tipula by the lack of verticils on the antennae (fig. 125, N, page 850). The immature stages are spent in rich organic mud. The pupae have a peculiar character in their elongate unequal breathing horns.

*Stygeropis fuscipennis* Loew

1865 *Stygeropis fuscipennis* Loew. Berl. Ent. Ztschr., vol. 9, p. 129.

*Stygeropis fuscipennis* is a medium-sized fly, with the thorax grayish brown, the pleura clearer gray, the abdomen brownish yellow, and the wings strongly tinged with brown. The wing venation is shown in Plate XLIII, 194, the ninth tergite of the male hypopygium in Plate XLIX, 255. These singular flies are characteristic inhabitants of marshy (helophytic) situations, and appear on the wing in July and August.

Genus **Aeshnasoma** Johnson

1909 *Aeshnasoma* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 115–116.

Aeshnasoma is a monotypic genus which is close to Longurio but probably separable from it. The fly is known only from the type station, New Jersey, where it is apparently not uncommon. Larvae were found in a cold stream near Riverton, New Jersey, by Johnson. They were not reared, but the striking resemblance to the larva of Longurio leaves no doubt as to their identity.

*Aeshnasoma rivertonensis* Johns.

1909 *Aeshnasoma rivertonensis* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 116, pl. 16, figs. 13–15.

*Aeshnasoma rivertonensis* is a large fly, nearly resembling *Longurio testaceus* but with the body coloration strongly reddish brown, including the wings, and with cell $M_1$ sessile. The abdomen of the male is 30 mm. in length, the wing 22 mm. The ninth tergite of the male hypopygium is shown in Plate XLIX, 257.

Genus **Longurio** Loew

1869 *Longurio* Loew. Berl. Ent. Ztschr., vol. 13, p. 3.

The small genus Longurio includes about six described species from widely separated areas of the earth, two being from eastern North America. It is probable that the species recently described by Edwards from Formosa is not a Longurio, as its hypopygium is very different from the peculiar type characteristic of this group (Plate LIII, 329). The immature stages are spent in sand or gravel near running water, usually in mountainous conditions. The bulky, semi-transparent larvae of *L. testaceus* are probably the largest crane-fly larvae to be found in eastern America; the writer is indebted to Mr. Hyslop for specimens which, altho not bred, can scarcely belong to any other species. The pupae are remarkable in their elongate breathing horns, these being nearly 20 mm. in length. The adult fly of *L. testaceus* is the largest crane-fly in eastern America, in the female sex even excelling the better-known *Holorusia grandis* of the West. It is found in cool, shaded woods, near streams, and is very wary and difficult to capture, usually alighting in the midst of a pile of brush or similar débris from which it cannot be swept with a net.

The following key divides the local species of Longurio:

Large, wing of male about 25 mm., abdomen 36 mm.; cell $M_1$ with its petiole very short [Berl. Ent. Ztschr., vol. 13, p. 3. 1869.] (Plate XLIII, 192, wing; Plate XLIX, 256, ninth tergite; Plate LIII, 329, lateral aspect of male hypopygium.) ..... *L. testaceus* Loew

Small, wing of male about 15 mm., abdomen 18 mm.; cell $M_1$ with its petiole elongated. [Proc. Acad. Nat. Sci. Phila., p. 605–606, pl. 27, fig. 32. 1914.] (Plate XLIII, 193.) *L. minimus* Alex.

## Genus **Nephrotoma** Meigen

1800 *Pales* Meig. Nouv. Class. Mouch. p. 14 (*nomen nudum*).
1803 *Nephrotoma* Meig. Illiger's Mag., p. 262.
1834 *Pachyrrhina* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 88.

The large genus Nephrotoma includes about one hundred and twenty-five species of medium-sized flies, which present a great uniformity of size and color but a considerable diversity in the structure of the male antennae. In many instances the species run close to those of Tipula, and the two genera are undoubtedly very close together. The writer (Alexander, 1915 b:466) has removed about six of the North American species of Nephrotoma from this genus and placed them in Tipula. As a rule the species of Nephrotoma are brilliantly colored with red, yellow, orange, or black, the body being shiny; in *N. macrocera* and to a lesser extent in the *tenuis* group, however, the body is dull. In the genus Tipula the colors are brown, gray, and yellow, and are dull, the only shiny species

being the ones that have been removed from Nephrotoma and referred to Tipula on other characters. The immature stages of the known species are spent in moist earth and in decaying wood.

The local species of Nephrotoma may be separated in accordance with the following key:

1. Thoracic stripes black or largely black ..... 2
   Thoracic stripes, if present, brownish or reddish ..... 8
2. Prescutum with the anterior lateral angles of the lateral stripes and the ends of the V-shaped suture deep velvety black; pleura with faint reddish markings. [*Pachyrrhina virescens* Loew. Berl. Ent. Ztschr., vol. 8, p. 62. 1864.] ..... *N. virescens* (Loew)
   Prescutum with the stripes uniform black thruout ..... 3
3. Wings with the ground color hyaline ..... 4
   Wings strongly tinged with brown or dusky, at least basally ..... 6
4. Lateral stripes on prescutum curved laterad at their anterior ends. [*Pachyrrhina incurva* Loew. Berl. Ent. Ztschr., vol. 7, p. 293. 1863.] (Plate XLIV, 204.) *N. incurva* (Loew)
   Lateral stripes on prescutum straight ..... 5
5. A small black spot on the vertex between the antennal bases; wings tipped with brown; abdominal segments banded with black. [*Pachyrrhina pedunculata* Loew. Berl. Ent. Ztschr., vol. 7, p. 293. 1863.] (Plate XLIV, 203.) ..... *N. pedunculata* (Loew)
   No small black spot between the antennal bases; wings not tipped with darker; abdominal segments trivittate, the lateral stripes interrupted, the median stripe continuous. [*Pachyrrhina vittula* Loew. Berl. Ent. Ztschr., vol. 8, p. 63. 1864.] *N. vittula* (Loew)
6. Lateral stripes on prescutum curved laterad at their anterior ends. [*Tipula lineata* Scop. Ent. Carniol., p. 320. 1763.] ..... *N. lineata* (Scop.)
   Lateral stripes on prescutum straight ..... 7
7. Prescutum with the ground color orange-yellow; scutellum and pleura mostly black; abdomen with black dorsal spots. [*Pachyrrhina lugens* Loew. Berl. Ent. Ztschr., vol. 8, p. 63. 1864.] (Plate XLIV, 202.) ..... *N. lugens* (Loew)
   Prescutum with the ground color obscure yellow; scutellum and pleura mostly yellow; abdomen with a black dorso-median stripe. [Proc. Acad. Nat. Sci. Phila., p. 467–468, pl. 16, fig. 1. 1915.] (Plate XLIV, 205.) ..... *N. penumbra* Alex.
8. Thoracic dorsum dull, opaque; antennae of male very elongated, the flagellum black. [*Tipula macrocera* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 24. 1823.] (Plate XLIV, 200.) ..... *N. macrocera* (Say)
   Thoracic dorsum more or less shiny; if at all opaque, the antennae of both sexes very short ..... 9
9. Antennal segments uniform in color ..... 10
   Antennal segments bicolorous ..... 17
10. A velvety black spot at the anterior end of the lateral prescutal stripe. [*Pachyrrhina punctum* Loew. Berl. Ent. Ztschr., vol. 7, p. 294. 1863.] ..... *N. punctum* (Loew)
    No velvety black spot at the anterior end of the lateral prescutal stripe ..... 11
11. Occiput opaque with a shining triangular spot in the middle ..... 12
    Occiput shining ..... 14
12. A black spot at each end of the V-shaped suture. [*Tipula ferruginea* Fabr. Syst. Antl., p. 28. 1805.] (Plate XLIV, 198.) ..... *N. ferruginea* (Fabr.)
    No black spots at the ends of the V-shaped suture ..... 13
13. Stigma pale, brownish yellow. [*Pachyrrhina occipitalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] ..... *N. occipitalis* (Loew)
    Stigma dark, blackish brown. [*Pachyrrhina gracilicornis* Loew. Berl. Ent. Ztschr., vol. 8, p. 66. 1864.] ..... *N. gracilicornis* (Loew)

14. Head with a shining triangular spot. [*Pachyrrhina occipitalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] ..... *N. occipitalis* (Loew)
Head unicolorous ..... 15
15. Wings strongly tinged with brown, especially along the costal region. [*Pachyrrhina okefenoke* Alex. Wash. Univ. Studies, p. 97–98. 1915.] ..... *N. okefenoke* (Alex.)
Wings not strongly brown along the costal region ..... 16
16. Head and thorax yellowish, almost opaque; color in life strongly greenish. [*Pachyrrhina tenuis* Loew. Berl. Ent. Ztschr., vol. 7, p. 297. 1863.] (Plate XLIV, 199.)
*N. tenuis* (Loew)
Head orange except the lateral margins of the vertex; thorax shining. [*Pachyrrhina sodalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 64. 1864.] ..... *N. sodalis* (Loew)
17. Segments of flagellum black at the base ..... 18
Segments of flagellum yellow at the base ..... 20
18. Wings strongly tinged with yellow; occiput without a clear, shining triangle. [*Pachyrrhina xanthostigma* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] (Plate XLIV, 201.) ..... *N. xanthostigma* (Loew)
Wings not strongly tinged with yellow; occiput with a clear, shining triangle ..... 19
19. Costal region hyaline; stigma dark brown. [*Pachyrrhina abbreviata* Loew. Berl. Ent. Ztschr., vol. 7, p. 295. 1863.] ..... *N. abbreviata* (Loew)
Costal region darker; stigma yellowish brown. [*Pachyrrhina suturalis* Loew. Berl. Ent. Ztschr., vol. 7, p. 295. 1863.] ..... *N. suturalis* (Loew)
20. Antennae with 13 segments. [*Pachyrhina breviorcornis* Doane. Ent. News, vol. 19, p. 178–179. 1908.] ..... *N. breviorcornis* (Doane)
Antennae with more than 13 segments ..... 21
21. Stigma yellowish brown; wing apex not darker; antennae of male 19-segmented. [*Pachyrrhina eucera* Loew. Berl. Ent. Ztschr., vol. 7, p. 296. 1863.] ..... *N. eucera* (Loew)
Stigma dark brown; wing apex distinctly darkened; antennae of male 16-segmented. [*Pachyrrhina polymera* Loew. Berl. Ent. Ztschr., vol. 7, p. 297. 1863.]
*N. polymera* (Loew)

After the above key was completed, Dietz (1918) published an extensive revision of the American species of the genus. A number of his new species are found within the faunal limits of this paper. The more salient characters of the regional species are here briefly summarized, and these species should be considered in addition to the key.

*Nephrotoma perdita* (Dietz). (Pages 116–117 of reference cited.)
Yellow; mouth parts and palpi yellow; occiput with a shiny brown pentagon; thoracic stripes black, narrowly margined with rusty, the lateral stripes curved outward and ending in an opaque black spot; wings grayish subhyaline, stigma brownish black. . Wing of female, 14.5 mm. (Manitoba, August.)

*N. hirsutula* (Dietz). (Pages 118–119 of reference.)
Very closely resembling *N. macrocera*, but with the wings sparsely pubescent. Eighth sternite of male deeply emarginate behind and with a digitiform lobe from the base of the notch. Wing of male, 12.5 mm. (Pennsylvania, May.)

*N. urocera* (Dietz). (Pages 119–120 of reference.)

*N. cornifera* (Dietz). (Pages 120–121 of reference.)
These two species are close to *N. okefenoke* but are easily separated by the male genitalia. They are from Virginia and North Carolina.

*N. calinota* (Dietz). (Pages 121–122 of reference.)
Yellow; antennal flagellum bicolorous; frontal prolongation of head dark brown medially; occiput opaque with a brown line; thoracic stripes silvery gray pruinose, the lateral stripes

outcurved and ending in a velvety black spot; wings grayish subhyaline, more yellowish basally, costal region brownish yellow. Wing of male, 11 mm. (Michigan and Maryland, June and July.)

*N. opacivitta* (Dietz). (Page 123 of reference.)

Similar to *N. calinota*, but with the antennae stout, the flagellum beyond the first segment blackish, the segments deeply incised beneath. Mesonotal prescutum with a median velvety black stripe; wings broad, tinged with brown; abdomen with a broad dark brown lateral stripe. Wing of male, 12 mm. (Manitoba.)

*N. evasa* (Dietz). (Pages 124–125 of reference.)

Yellow; antennae entirely yellowish; occiput with a shiny, broadly triangular spot; prescutum with an anterior median black mark; abdominal tergites margined posteriorly with yellowish brown. Wing of female, 13.5 mm. (Michigan, July.)

*N. festina* (Dietz). (Pages 126–127 of reference.)

Pale yellow; antennae very slender, the flagellar segments yellow, the outer ones more yellowish brown; occiput shiny; wings tinged with yellowish, the costal area pale yellow, the stigma brown; abdomen on either side with a row of black dashes. Wing of male, 12.5 mm. (Pennsylvania and Maryland, July and August.)

*N. temeraria* (Dietz). (Page 128 of reference.)

Yellow; antennae entirely yellowish; occiput opaque with a narrow shiny brown line; wings faintly tinged with grayish yellow, the costal area and along the veins more yellowish, the stigma brown; abdomen with a broad, pale brown, dorsal stripe, and with a row of black dashes along each lateral margin of the tergum. Wing of female, 13 mm. (Michigan, July.)

*N. cingulata* (Dietz). (Pages 131–133 of reference.)

Close to *N. xanthostigma*. Antennae of male elongated, the flagellar segments bicolorous, dark brown at base; thoracic dorsum highly polished, testaceous, the stripes poorly defined; wings strongly tinged with yellow as in *N. xanthostigma*, the costal region and along vein *Cu* more saturated, the stigma pale brown. Wing of male, 11 mm. (Pennsylvania, July and August.)

*N. obliterata* (Dietz). (Pages 133–134 of reference.)

Close to *N. xanthostigma*. Flagellar segments of antennae bicolorous, the segments dusky, blackish at base; occiput shiny; thorax sulfur yellow, the stripes rusty, the transverse suture black medially; wings grayish subhyaline, stigma yellowish; abdomen with a dark brown dorsal stripe and lateral rows of spots. Wing of male, 12.5 mm. (Ottawa, Michigan, and Pennsylvania, July and August.)

*N. wyalusingensis* (Dietz). (Pages 134–135 of reference.)

Close to *N. obliterata*. Head dark testaceous; flagellar segments of antennae bicolorous, yellowish brown, black at base; occiput shiny, a small brown spot at base; prescutum shiny yellow, the stripes dark rusty; wings pale brown, the costal region yellowish; abdomen dark testaceous, the lateral margins of tergites and the posterior margins of segments bordered with black. Wing of male, 12.5 mm. (Pennsylvania, August.)

*N. approximata* (Dietz). (Pages 136–137 of reference.)

Closely resembling *N. cingulata*, but with the flagellar segments brown, rusty at base. Antennae of male long, slender; occiput shiny with a dark brown stripe; thoracic stripes rusty brown; wings grayish, stigma brownish yellow; abdomen with black lateral stripes, the segments margined posteriorly with brown. Wing of male, 12 mm. (Pennsylvania, August.)

*N. stigmatica* (Dietz). (Pages 137–138 of reference.)

Close to *N. breviorcornis*. Honey yellow; antennae of male short, the flagellar segments bicolorous, segments brown, yellow at base; thoracic stripes dark rusty; wings yellowish subhyaline, the costal area and along *Cu* more saturated, the stigma dark; abdomen with a brown dorsal stripe and more or less complete lateral stripes, a mid-ventral row of small black spots on the sternites. Wing of male, 12.5 mm. (Pennsylvania, August.)

## Genus **Tipula** Linnaeus

1758 *Tipula* Linn. Syst. Natur., vol. 10, p. 585.
1864 *Anomaloptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 218.
1887 *Oreomyza* Pokorny. Wien. Ent. Ztg., vol. 6, p. 50.

Tipula is the largest genus of crane-flies. It includes some six hundred and fifty described species, found in most parts of the world and very abundant on most of the continental areas but rare or lacking on many of the smaller oceanic islands. Obviously such a group of very closely related species presents considerable difficulty in classification. The keys to the species of any region are so cumbersome as to be almost unworkable, and yet it is very difficult to lessen this problem. In the present paper the geographical area has been considerably restricted and the number of included species is thus reduced. It is further reduced by the omission of species that have not been definitely recognized since their original characterization, thus eliminating species described by Walker, Macquart, and others; the inclusion of these species in keys is altogether guesswork, and it is far better to omit them until their types can be examined and the determination made final. The species described by Say, Doane, and Loew are fairly well known and very few of these are in doubt.

In order to supplement the keys, practically all the species are figured. In those forms having a characteristic wing pattern, it is the wing that is shown; while in those that evince notable characters of the male hypopygium, various parts of this organ are figured. In this genus, as in many others, it is almost impossible to separate the females unless they have been taken in copulation with the males.

The life histories of species in this genus are diverse, ranging from strictly aquatic forms to those occurring in wet mud, in moist soil, and in decaying wood.

An attempt is herein made to divide the local species into groups, the following characters being considered in making this division:

*Color characters*, as in the *collaris* group, in which the body coloration is strikingly like that in Nephrotoma, and the dimorphic groups (*T. fuliginosa*, *T. annulicornis*), with light-colored males and brown or black females.

*Antennae*, whether longer in the male than in the female, or short in both sexes.

*Wings*: pubescence in the apical cells, as in the subgenera Trichotipula, Cinctotipula, and Odontotipula; the features of wing venation, such as the atrophy of the tip of vein $R_2$; the retention of the *m-cu* cross-vein and its position in regard to the fork of $M$; the shape of the cell *1st* $M_2$; the wing pattern, which divides the species into three groups, as follows:

*striatae*, wings streaked longitudinally;
*marmoratae*, wings cross-banded or spotted in various ways;
*subunicolores*, wings hyaline or unicolorous.

*Male hypopygium*, whether the sclerites of the ninth segment are separate, or the tergite is fused with the sternite, or all the sclerites are fused into a continuous ring. The primitive character is to have a separate tergite, pleurite, and sternite, and specialization in the organ is shown by the fusion of these parts. The pleurite is first lost, by fusing with the sternite, but a part of the pleural suture is retained in all except the most specialized forms. The culmination of the organ in this genus is the fusion of the tergite with the already fused sterno-pleurite so as to form a continuous ring. The eighth sternite shows many curious modifications, which have already been discussed (p. 873).

*Female hypopygium*, which is much more homogeneous than the male hypopygium but which still shows many peculiar modifications and tendencies. There may be a sudden narrowing of the organ, as in *T. besselsi*, or the valves may be shortened and fleshy, and feebly chitinized, as in the *collaris* and *bicornis* groups. The most striking modification apparently is that seen in the *arctica* group, in which the ovipositor has two valves lying transversely and with the outer margins variously serrated.

Four subgenera are included in the genus, classified as follows:

A. Subgenus *Trichotipula* Alex.— Apical cells of the wings with abundant short hairs; coloration dull, as in Oropeza, but vein $R_2$ persistent for its entire length.

*Tipula* (*Trichotipula*) *oropezoides* Johns.

B. Subgenus *Cinctotipula* Alex.— Apical cells of the wings with a sparse, short pubescence; coloration dark brown, the mesonotum with pale stripes; ninth tergite with the caudal margin concave; antennae of the male elongated.

*Tipula* (*Cinctotipula*) *algonquin* Alex.
*Tipula* (*Cinctotipula*) *unimaculata* (Loew)
*Tipula* (*Cinctotipula*) *dorsolineata* Doane

C. Subgenus *Odontotipula* Alex.— Apical cells of the wings with a very sparse, short pubescence, most evident in cell $R_5$; coloration bright shiny yellow and red, as in species of Nephrotoma; antennae of the male short.

*Tipula* (*Odontotipula*) *unifasciata* (Loew)

D. Subgenus *Tipula* Linn.— No pubescence in the apical cells of the wings. This subgenus is divided into twenty-two groups, as follows:

1. The *collaris* group.— Coloration shiny black and yellow, as in species of Nephrotoma; wings with the *m-cu* cross-vein beneath the middle of cell *1st* $M_2$; female ovipositor with the valves short and fleshy.

*Tipula collaris* Say
*T. nobilis* (Loew)

2. The *pachyrhinoides* group.— Similar to the preceding in coloration; wings with the *m-cu* cross-vein nearer to the fork of *M* than to the medial cross-vein; female ovipositor with the valves elongate and chitinized.

*T. pachyrhinoides* Alex.

3. The *bicornis* group.— Nasus very short to indistinct; coloration dull yellow to brownish yellow, with the thoracic stripes usually distinct; venation with cell *1st* $M_2$ very small and pentagonal; male hypopygium with the ninth tergite usually tumid; female ovipositor with the valves short, blunt, subfleshy.

*T. bicornis* Forbes
*T. megaura* Doane
*T. morrisoni* Alex.
*T. parshleyi* Alex.
*T. johnsoniana* Alex.

4. The *valida* group. — A heterogeneous collection of subgroups, as follows:

a. The *valida* subgroup.— Very large species; the eighth sternite with prominent lateral lobes and a depressed median lobe.

*T. valida* Loew
*T. hirsuta* Doane

b. The *umbrosa* subgroup.— Large species; the eighth sternite provided with conspicuous lateral lobes, and the caudal area between with two chitinized points.

*T. umbrosa* Loew
*T. flavoumbrosa* Alex.

c. The *australis* subgroup.— Medium-sized species; the lateral lobes of the eighth sternite (*T. australis*) tending to disappear (*T. dietziana*) and pass into the fourth subgroup.

*T. australis* Doane
*T. dietziana* Alex.

d. The *submaculata* subgroup.— A great assemblage of forms, including the majority of the *subunicolores*. Wing practically unicolorous (except in *T. huron*) but the obliterative streak well marked; ninth tergite variously notched medially; eighth sternite provided with tufts of short to long hairs, in the specialized forms (*T. tuscarora*) passing into a single powerful bristle on either side.

*T. mainensis* Alex.
*T. mingwe* Alex.
*T. georgiana* Alex.
*T. monticola* Alex.
*T. translucida* Doane
*T. cincticornis* Doane
*T. penicillata* Alex.
*T. triton* Alex.
*T. submaculata* Loew
*T. tuscarora* Alex.
*T. huron* Alex.

5. The *besselsi* group.— A small group of high arctic species; coloration blue-gray; head, thorax, and coxae with abundant long white hair; valves of the ovipositor suddenly narrowed, weak.

*T. besselsi* O. S.
*T. piliceps* Alex.

6. The *aperta* group.— A reduced species, with the venation in process of atrophy, the medial cross-vein lacking.

*T. aperta* Alex.

7. The *apicalis* group.— An isolated species that has probably come from the *valida* group; wing broadly tipped with brown; ninth tergite deeply notched medially. This species is possibly closer to *T. mainensis* than this grouping would indicate.

*T. apicalis* Loew

8. The *hermannia* group.— Wings sparsely blotched with darker; ninth tergite with a prominent, compressed, median lobe; antennae of the male elongate; not dimorphic.

*T. hermannia* Alex.

9. The *annulicornis* group.— Dimorphic, the males light-colored, the females dark brown, the wings practically unicolorous; male antennae elongate to very elongate (*T. taughannock*); ninth tergite with a conspicuous median lobe and more or less prominent lateral lobes.

*T. annulicornis* Say
*T. taughannock* Alex.

10. The *fuliginosa* group.— Dimorphic, the males light-colored (*T. speciosa*), the females very dark brown (*T. fuliginosa*) with white markings; ninth tergite asymmetrical, the right pleurite produced caudad in a prominent two-cleft arm; ninth tergite deeply notched medially.

*T. fuliginosa* (Say)

11. The *trivittata* group.— Wings conspicuously cross-banded, an uninterrupted white band beyond the cord; ninth tergite notched, with a small tooth at the base of the notch.

*T. trivittata* Say
*T. angulata* Loew
*T. entomophthorae* Alex.

12. The *subfasciata* group.— Wings conspicuously cross-banded, an uninterrupted white band beyond the cord; tip of vein $R_2$ atrophied. The species of this group are evidently derived from the last preceding group, being reduced forms.

*T. subfasciata* Loew
*T. penobscot* Alex.

13. The *hebes* group.— A well-marked group of species, including forms with elongate antennae in the male sex and those with the antennae short in both sexes; hypopygium elongated and curiously upturned at an angle with the remainder of the abdomen; eighth sternite three-lobed, the margins clothed with golden-yellow hairs; wing pattern a peculiar spotting and blotching of browns, grays, and whites.

*T. hebes* Loew
*T. latipennis* Loew
*T. grata* Loew
*T. afflicta* Dietz
*T. helderbergensis* Alex.

14. The *macrolabis* group.— Ninth pleurite greatly produced caudad into finger-like lobes; wing pattern spotted, the costal region with four larger blotches.

*T. macrolabis* Loew
*T. macrolaboides* Alex.

*T. loewiana* Alex. may be considered as coming close to this group, the ninth pleurite being produced caudad as a short, subspatulate lobe.

15. The *arctica* group.— A well-defined group of species; female ovipositor with but two functional valves, which are strongly serrated along their outer margins; ninth tergite showing two distinct types, in one of which (*T. arctica, T. alticola*) the sclerite is very small and the caudal margin is evenly concave and heavily chitinized, in the second (*T. longiventris, T. caroliniana*) the tergite is feebly chitinized and the sclerite has a small dorsal transverse knob at about midlength.

*T. arctica* Curt.
*T. labradorica* Alex.
*T. serrulata* Loew
*T. septentrionalis* Loew
*T. longiventris* Loew
*T. caroliniana* Alex.
*T. fultonensis* Alex.
*T. alticola* Alex.

16. The *angustipennis* group.— A large group of species; wings spotted with white on a brown or a grayish ground; eighth sternite usually unarmed, but in some species (*T. serta*) with a small median lobe, in others (*T. senega*) with prominent fleshy lateral lobes; ninth tergite variously shaped; outer pleural appendage broad and fleshy; female ovipositor with the valves usually elongated, much shorter and sublyriform in *T. senega*, never serrated.

*T. balioptera* Loew
*T. centralis* Loew
*T. canadensis* Loew
*T. ternaria* Loew
*T. angustipennis* Loew
*T. ignota* Alex.
*T. serta* Loew
*T. senega* Alex.

17. The *marmorata* group.— Wing pattern pale, marmorate gray, brown, and hyaline; *m-cu* cross-vein usually distinct and rather close to the fork of *M*.

*T. fragilis* Loew
*T. ignobilis* Loew

18. The *abdominalis* group.— An extensive group of large flies, including some of the largest in the genus. The species are more numerous in the West and thence southward (*T. oblique-fasciata, T. craverii, T. commiscibilis, T. abluta, T. rupicola, T. albimacula*, and

others). Wing pattern characteristic, with whitish or hyaline spots at the ends of the veins at the wing margin; ninth tergite tending to be notched, and often rather massive.

*T. abdominalis* (Say)

19. The *dejecta* group.— Ninth tergite with two lobes on the caudal margin, in *T. iroquois* slender and lying parallel, in *T. dejecta* more divergent; ninth tergite strongly fused with the sternite in *T. dejecta*, the condition found in the remaining groups to be considered.

*T. iroquois* Alex.
*T. dejecta* Walk.
*T. aprilina* Alex.

20. The *tephrocephala* group.— Sclerites of the ninth segment fused into a continuous ring; ninth tergite with two slender parallel lobes on the caudal margin.

*T. tephrocephala* Loew
*T. cayuga* Alex.

21. The *tricolor* group.— Species with striate wings. This group is divisible into the following two subgroups, which pass readily into each other:

a. The *tricolor* subgroup.— Wings with a heavy striate pattern.

*T. sayi* Alex.
*T. tricolor* Fabr.
*T. caloptera* Loew
*T. bella* Loew
*T. fraterna* Loew
*T. strepens* Loew
*T. eluta* Loew
*T. conspicua* Dietz
*T. ludoviciana* Alex.
*T. sackeniana* Alex.
*T. vicina* Dietz

b. The *perlongipes* subgroup.— Wings subhyaline.

*T. perlongipes* Johns.
*T. sulphurea* Doane
*T. kennicotti* Alex.

The *tricolor* group has the sclerites of the ninth segment fused into a continuous ring; the ninth tergite has a single broad, depressed, median lobe, which in some species is indistinctly cut in two by a median split.

22. The *cunctans* group.— Sclerites of the ninth segment fused into a continuous ring; ninth tergite with a conspicuous median notch.

*T. cunctans* Say
*T. ultima* Alex.

The local species of the genus Tipula may be separated in accordance with the following key:

1. Wings with a distinct pubescence in the apical cells.....2
   Wings without pubescence in the apical cells. (Subgenus *Tipula* Linn.).....5
2. Pubescence of wings abundant, including all the apical cells from $R_1$ to $M_4$; coloration dull as in species of Oropeza; antennae black, the scape light yellow; thorax brownish gray, the prescutum with three darker brownish gray stripes; basal deflection of $Cu_1$ and the *m-cu* cross-vein at or near the fork of $M$; male hypopygium with each caudo-ventral angle of the ninth sternite prolonged caudad into a pale, slender, finger-like lobe. [Proc. Boston Soc. Nat. Hist., vol. 34, no. 5, p. 131. 1909.] (Plate XLIII, 195, wing; Plate XLIX, 258, ninth tergite; Plate LIII, 330, lateral aspect of male hypopygium.) (Subgenus *Trichotipula* Alex.).....*T. oropezoides* Johns.
   Pubescence of wings less abundant, not extending beyond cells $R_3$, $R_5$, $M_1$, and $M_2$ and confined to the centers of the cells; coloration usually bright as in Nephrotoma, or else the prescutum dark-colored with pale stripes.....3

3. Coloration bright shiny yellow, reddish, and black; vertex shiny, with a black spot along the inner margin of each eye and a linear dark brown median area; thorax yellow with three shiny reddish stripes, the middle one narrowly divided; male antennae very short, not attaining the wing base; pubescence of the wings confined to cell $R_4$; male hypopygium with the ninth sternite produced caudad in two powerful tooth-like lobes. [*Pachyrrhina unifasciata* Loew. Berl. Ent. Ztschr., vol. 7, p. 294. 1863.] (Plate XLIV, 206, wing; Plate XLIX, 262, ninth tergite.) (Subgenus *Odontotipula* Alex.) ..... *T. unifasciata* (Loew)

Coloration dull brown and yellow; vertex opaque without black marks; prescutum dull, dark-colored with paler stripes, the median one at least well indicated; male antennae elongate, reaching about to the base of the abdomen; pubescence of the wings more extensive, from cell $R_2$ to $M_3$. (Subgenus *Cryptotipula* Alex.) ..... 4

4. Antennae with the flagellum bicolorous, the basal swelling of each segment black, the elongate pedicel dull yellow; abdomen without distinct crossbands to the segments. [*Pachyrrhina unimaculata* Loew. Berl. Ent. Ztschr., vol. 8, p. 64. 1864.] (Plate XLIII, 196, wing; Plate XLIX, 259, ninth tergite.) ..... *T. unimaculata* (Loew)

Antennae with the flagellum unicolorous; abdomen with the caudal half of the segments dark brown, the basal half more yellowish producing a banded appearance. [Proc. Acad. Nat. Sci. Phila., p. 469–471, pl. 16, fig. 2. 1915.] (Plate XLIII, 197, wing; Plate XLIX, 260, ninth tergite; Plate LIII, 324, eighth sternite.) .. *T. algonquin* Alex.

5. Coloration as in Nephrotoma — shiny, contrasting blacks, yellows, and reddish browns .. 6

Coloration dull brown, gray, or blackish, not at all shiny ..... 8

6. Head with a linear black median mark extending from between the antennal bases to the occiput, sides of the abdomen without patches of light silvery gray; female ovipositor, elongate, pointed, the valves chitinized. [Proc. Acad. Nat. Sci. Phila., p. 471–472, pl. 16, fig. 3. 1915.] (Plate XLIV, 209, wing.) ..... *T. pachyrhinoides* Alex.

Head without a black median line; sides of the abdomen with patches of light silvery, gray pruinosity; female ovipositor very blunt, truncate, the valves not chitinized, simulating the hypopygium of the male (*collaris* group) ..... 7

7. Head orange-yellow, the occiput with a grayish black spot; prescutum orange-yellow with three dull gray-black stripes; posterior margin of the postnotum, and the apical half of the first abdominal segment, light gray. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 25. 1823.] (Plate XLIV, 207, wing.) ..... *T. collaris* Say

Head orange-yellow, with a large brownish orange spot on each side of the vertex touching the inner margin of the eye; prescutum shiny, light honey-yellow, with three shiny jet-black or reddish black stripes; posterior margin of the postnotum, and the apical half of the first abdominal segment, not light gray; wings yellowish, the cord and the apex narrowly seamed with brown. (*Pachyrrhina nobilis* Loew. Berl. Ent. Ztschr., vol. 8, p. 62. 1864.) (Plate XLIV, 208, wing; Plate XLIX, 261, ninth tergite.) ..... *T. nobilis* (Loew)

8. Wings striped or streaked longitudinally with brown or reddish brown, this including the costal region and along $Cu$; cell $M$ usually hyaline or nearly so; male hypopygium with the sclerites of the ninth segment fused into a continuous ring (*tricolor* group) ..... 9

Wings not striped nor streaked as above, the costal margin in some cases darkened but if so with no brown seams on the other veins ..... 14

9. Wings with cell $R_1$ hyaline or nearly so, at least on its apical half, thus being continuous or nearly so with the area in cell $M$ ..... 10

Wings with cell $R_1$ infuscated, concolorous with cells $R_2$ and $M_1$ ..... 13

10. Large species, wing of male over 20 mm.; base of cell $R_1$ darkened ..... 11

Smaller species, wing of male under 18 mm.; cell $R_1$ hyaline ..... 12

11. Large, wing of male 25 mm., and darker-colored; prescutal stripes heavily margined with dark brown; antennae short, not attaining the wing base, dark brown thruout; abdominal tergites with a dark brown sublateral stripe; wings with the pattern clear-cut, a bright yellow spot in cell *1st* $R_2$; cells $M_1$, $M_2$, $M_4$, and $Cu_1$ infuscated; male

hypopygium with the ninth tergite (Plate XLIX, 267) having a slender median lobe, truncated at the apex, with a conspicuous chitinized claw on either side of the tergal region. [Berl. Ent. Ztschr., vol. 7, p. 292. 1863.] (Plate XLV, 214, wing.)
*T. caloptera* Loew

(Two species are apparently confused under this name; true *caloptera* has the bases of cells $M_1$, $M_2$, and $M_4$ pale, as figured, and the male hypopygium lacks the clawlike appendage on either side of the median lobe of the ninth tergite.)

Smaller, wing of male 23 mm. or less, and paler-colored; prescutal stripes not heavily margined with brown; antennae longer, extending nearly to the base of the abdomen, bicolorous; abdominal tergites without a dark brown sublateral stripe; wings without a conspicuous yellow spot in cell *1st* $R_1$; cells $M_1$, $M_2$, $M_4$, and $Cu_1$ hyaline basally; male hypopygium with the ninth tergite (Plate XLIX, 264) having a broad median lobe, rounded at the apex; no lateral claws on the tergal region. [Berl. Ent. Ztschr., vol. 7, p. 291. 1863.] (Plate XLV, 215, wing.)..... *T. strepens* Loew

12. Antennae short, with only the basal segments of the flagellum distinctly bicolorous; wing pattern more clear-cut, the costal stripe broader and darker brown, vein *Cu* and the basal deflection of $Cu_1$ with a broad dark brown seam. [Berl. Ent. Ztschr., vol. 7, p. 291. 1863.] (Plate XLV, 216, wing; Plate XLIX, 265, ninth tergite.)
*T. bella* Loew

Antennae longer, with all except the terminal segments of the flagellum distinctly bicolorous; wing pattern less distinct and rather poorly defined, the brown stripes and seams much paler. [Berl. Ent. Ztschr., vol. 7, p. 290. 1863.] (Plate XLV, 217, wing.)..... *T. eluta* Loew

13. White obliterative streak before the wing cord passing beyond cell *1st* $M_2$ and almost reaching the wing margin; male hypopygium having the region of the ninth tergite without a brush of bristles on its lateral part. [Berl. Ent. Ztschr., vol. 8, p. 56. 1864.]
*T. fraterna* Loew

White obliterative streak before the wing cord ending in the extreme base of cell $M_4$; male hypopygium having the region of the ninth tergite (Plate XLIX, 263) with a brush of long, stiff, reddish bristles on its lateral part. [Ent. Syst., vol. 4, p. 235. 1794.] (Plate XLV, 218, wing.)..... *T. tricolor* Fabr.

(*Tipula vitrea* v. d. W. [Tijd. Ent., vol. 24, p. 150, pl. 15, fig. 5, 1881] is very close to *T. tricolor* but may be a good species. The description of *T. vitrea* calls for a testaceous abdomen with a brown lateral stripe, while in *T. tricolor* the abdomen is concolorous thruout.).

14. Costal margin of wings dark brown; male hypopygium with the sclerites of the ninth segment fused into a continuous ring..... 15

Costal margin of wings not dark brown..... 16

15. Wings with the brown costal margin including the base and the cephalic parts of cells *R* and $R_1$; male hypopygium with the ninth tergite (Plate XLIX, 266) having a low, broad, depressed, median protuberance (*tricolor* group). [*T. sayi* Alex., Psyche, vol. 18, p. 194, 1911. *T. costalis* Say, preoccupied, Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23, 1823.] (Plate XLV, 219, wing.)..... *T. sayi* Alex.

Wings with the brown costal margin including cells *C* and *Sc* only; male hypopygium with the ninth tergite (Plate L, 274) having a median notch. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23. 1823.] (Plate XLV, 220, wing; Plate LIII, 332, lateral aspect of male hypopygium.)..... *T. cunctans* Say

16. Wings strongly tinged with yellow; a brownish cloud at the end of vein *2d A*; male hypopygium with the sclerites of the ninth segment fused into a continuous ring and the tergal region (Plate L, 273) notched medially. [*T. ultima* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. flavicans* Fabr., Syst. Antl., p. 24, 1805; written *flavescens*.] (Plate XLVII, 232, wing; the figure of the wing reproduced far too dark to give an idea of the pattern in this species. Plate LIII, 333, lateral aspect of male hypopygium.)..... *T. ultima* Alex.

Wings not strongly tinged with yellow, or if so without a brown cloud at the end of vein *2d A*..... 17

17. Wings spotted, banded, clouded, or tipped with brown or gray.....18
Wings unicolorous — hyaline, yellowish, or dark brown, in many cases, however, with the stigmal spot present; usually with a pale vitreous obliterative streak at or before the cord, extending from before the stigma to the region of cell *1st* $M_2$ or beyond; in some cases the costal region a little darkened, and perhaps a vitreous spot beyond the stigma in the base of cell $R_2$.....68
18. Tip of vein $R_2$ atrophied.....19
Tip of vein $R_2$ present, reaching the wing margin.....20
19. Wings long and narrow, in the male 14 mm. long; cell *1st* $M_2$ elongate, as long as or longer than cell $M_1$; blotch at the origin of the sector connected with the blotches in cell $R$. [Berl. Ent. Ztschr., vol. 7, p. 282. 1863.] (Plate XLVIII, 248, wing.)
*T. subfasciata* Loew
Wings short and broad, in the male 11.6 mm. long; cell *1st* $M_2$ short and broad, about two-thirds the length of cell $M_1$; a small brown spot at the origin of the sector; a dark spot at the base of the wing. [Proc. Acad. Nat. Sci. Phila., p. 472–474, pl. 16, fig. 4. 1915.] (Plate XLVIII, 247, wing; Plate L, 275, ninth tergite; Plate LIII, 334, lateral aspect of male hypopygium.).....*T. penobscot* Alex.
20. Wings with the apex broadly dark brown, extending from the outer end of cell $R_2$ to the end of cell $M_2$; no brown markings proximad of the cord; body coloration yellowish brown; scape of the antennae bright yellow; wing under 15 mm. [Berl. Ent. Ztschr., vol. 7, p. 277. 1863.] (Plate XLVIII, 254, wing; Plate LI, 302, ninth tergite; Plate LIV, 342, lateral aspect of male hypopygium.).....*T. apicalis* Loew
Wings with the dark markings not confined to the apex, or if the tip is darkened the coloration of the body is gray and the scape of the antenna is dark brown (*T. iroquois*) or the size of the fly is larger (*valida* group, wings over 18 mm.).....21
21. Wings banded brown and white, with a broad, uninterrupted white crossband beyond the stigma, extending from the end of cell *2d* $R_1$ to the middle of cell $M_4$, or beyond to the wing margin.....22
Wings without an uninterrupted white crossband beyond the stigma.....23
22. Smaller species, wing of male less than 15 mm.; antennal flagellum bicolorous; thorax gray with four broad brownish stripes; wings with the white fasciae narrow; male hypopygium with the ninth tergite (Plate LI, 291) narrowly notched medially. [Berl. Ent. Ztschr., vol. 8, p. 61. 1864.] (Plate LIV, 340, lateral aspect of male hypopygium.).....*T. angulata* Loew
Larger, wing of male over 15 mm.; antennal flagellum unicolorous; thorax gray with an interrupted pattern of dots and narrow brown lines; wings with the white fasciae broad, the basal one especially broad; male hypopygium with the ninth tergite (Plate LI, 294) broadly and shallowly notched caudally, bearing a more or less bifurcate median tooth. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 26. 1823.] (Plate XLVI, 226, wing.).....*T. trivittata* Say
23. Large, length of male over 25 mm.; vertex light yellow; thoracic dorsum with a velvety black pattern margined with paler, producing an ocellate appearance; abdominal tergites bright orange with a broad brownish black stripe on either side; segments 7 to 9 dark brownish black. [*Ctenophora abdominalis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLV, 210, wing; Plate LI, 299, ninth tergite.)
*T. abdominalis* (Say)
Smaller, length of male under 20 mm.; not colored as above.....24
24. Males (as known).....25
Females (as known).....49
25. Coloration bright orange, the thoracic dorsum without darker stripes; wings yellowish basally, more clouded with brown apically; a small brown spot at the base of the wing and another at the origin of the sector; antennae bicolorous; male hypopygium asymmetrical, the right pleurite produced caudad into a prominent two-cleft arm. [*Ctenophora fuliginosa* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLVIII, 245, wing of male; Plate LI, 289, ninth tergite.)...*T. fuliginosa* (Say)
Coloration not as above.....26

26. Male hypopygium with the ninth tergite (Plate L, 287) produced caudad into a compressed median lobe; antennae elongate, bicolorous; wings with an extensive brownish gray blotch before the cord, occupying the ends of cells *R* and *M* and the lower basal angle of cell $Cu_1$; a broad cloud on the petiole of cell $M_1$; prescutum light gray, with four broad dark gray stripes. [*T. hermannia* Alex., Proc. Acad. Nat. Sci. Phila., p. 480, 1915. *T. fasciata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 279, 1863.] (Plate XLV, 211, wing; Plate LIV, 343, lateral aspect of male hypopygium.)
*T. hermannia* Alex.

Male hypopygium not as above ..... 27

27. Wings with a pale gray tinge, more brownish in cell *M* along vein *Cu*; hyaline spots in the anal cells, at two-thirds the length of cell $M_1$, before the stigma, and an interrupted band before the cord extending to cell *1st* $M_2$; body coloration gray, the prescutum with four dark brown stripes; male hypopygium small, not conspicuously elongated or enlarged (*marmorata* group) ..... 28

Wings brown or dark gray, with a pattern of white or hyaline spots and blotches .... 29

28. Stripes on the prescutum ending at the level of the pseudosutural foveae, the median pair blunt at their anterior ends; apical tergites of the abdomen not conspicuously darkened. [Berl. Ent. Ztschr., vol. 7, p. 279. 1863.] (Plate XLVIII, 250, wing; the figure is much darker than in normal specimens. Plate LI, 297, ninth tergite.)
*T. fragilis* Loew

Median stripes of the prescutum extending about to the anterior margin of the sclerite, deeply bifid at the anterior end; apical segments of the abdomen largely blackish. [Berl. Ent. Ztschr., vol. 7, p. 280. 1863.] (Plate LI, 298, ninth tergite.)
*T. ignobilis* Loew

29. Male hypopygium with the ninth segment elongate-cylindrical, strongly upturned; eighth sternite with the caudal margin tripartite and clothed with yellow hairs; wings with a variegated brown, gray, and white pattern (*hebes* group) ..... 30

Male hypopygium with the ninth segment not strongly upturned ..... 33

30. Antennae elongated in the male, extending about to the base of the abdomen ..... 31

Antennae short in both sexes, extending about to the wing root ..... 32

31. Antennal flagellum bicolorous; bladelike processes of the male hypopygium not elongated nor spiraliform. [Berl. Ent. Ztschr., vol. 7, p. 285. 1863.] (Plate XLVIII, 249, wing.) ..... *T. hebes* Loew

Antennal flagellum uniform dark brown, at least apically; bladelike processes of the male hypopygium elongate, spiraliform. [Berl. Ent. Ztschr., vol. 8, p. 60. 1864.] (Plate LI, 293, ninth tergite.) ..... *T. latipennis* Loew
(*T. ottawaensis* Dietz is the same as *T. latipennis* Loew.)

32. Antennal flagellum yellowish brown; appendiculate process of the male hypopygium slender and pointed apically. [Berl. Ent. Ztschr., vol. 7, p. 281. 1863.] (Plate LI, 292, ninth tergite.) ..... *T. grata* Loew

Antennal flagellum dark brown; appendiculate process of the male hypopygium broad, obtusely pointed at the apex. [*T. afflicta* Dietz, Trans. Amer. Ent. Soc., vol. 40, p. 351–352, pl. 13, figs. 5, 6, pl. 14, fig. 2, 1914, as *T. suspecta* Dietz.] .. *T. afflicta* Dietz
(*T. afflicta* Dietz is close to *T. grata* Loew but apparently separable from it.)

33. Wing with four large brown subequidistant blotches along the radial vein, the second at the origin of the sector, the fourth on vein $R_3$; male hypopygium with the ninth pleurite greatly produced into slender, chitinized, digitiform processes (*macrolabis* group) ..... 34

Wings variously marked but without four large brown subequidistant blotches along the radial vein; male hypopygium with the ninth pleurite not greatly produced .... 35

34. Ninth tergite (Plate LI, 295) rather squarely truncated across the caudal margin, with a sharp median tooth; apex of the ninth pleurite ending in acute teeth (Plate LIII, 322). Northeastern North America. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] (Plate XLVII, 233, wing; the brown blotches along *R* do not show clearly in the figure.) ..... *T. macrolabis* Loew

Ninth tergite (Plate LI, 296) not square across the caudal margin; the sharp median tooth subtended on either side by a flattened divergent lobe; apex of the ninth pleurite rounded and blunt, not toothed (Plate LIII, 323). Western North America. [Can. Ent., vol. 50, p. 69–70. 1918.] ..... *T. macrolaboides* Alex.

35. Wings with the apex narrowly and irregularly darkened; narrow brown seams along the cord; antennae dark brown thruout; prescutum gray, with darker gray stripes which are narrowly margined with dark brown; pleura clear light gray; male hypopygium with the ninth tergite large (Plate LI, 300), the caudal margin produced into two short, parallel lobes, one on either side of the median line. [*T. iroquois* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. cincta* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 288, 1863.] (Plate XLVIII, 252, wing; Plate LIV, 344, lateral aspect of male hypopygium.) ..... *T. iroquois* Alex.

Wings not colored as above ..... 36

36. Wing apex infuscated; a dark spot at the origin of the sector; male hypopygium with the ninth tergite (Plate LII, 317) prominent, deeply notched, the lateral lobes acute; medium-sized, wing 18 mm. or less; antennae bicolorous. [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) ..... *T. submaculata* Loew

Not as above; if the wing pattern is as described (*valida* group), the size is much larger — wing of male 20 mm. ..... 37

37. Large, wing of male 20 mm.; wings with the apices light or dark brownish gray; male hypopygium greatly enlarged (*valida* group) ..... 38

Smaller, wing of male under 18 mm.; wings with a heavy brown and white or grayish brown and white pattern ..... 39

38. Ninth tergite (Plate LI, 303) with the lateral lobes more slender and pronounced; eighth sternite without a long brush of hairs; wing apex darker, brownish. [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] (Plate XLVII, 237, wing; the reproduction of the figure is much too dark.) ..... *T. valida* Loew

Ninth tergite (Plate LI, 304) with the lateral lobes shorter and less evident; eighth sternite with a tuft of long yellow hairs; wing apex light gray, scarcely darker than the basal part of the wing. [Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.] (Plate LIV, 345, lateral aspect of male hypopygium.) ..... *T. hirsuta* Doane

39. Ninth tergite of the male with a dorsal black chitinized projection lying transversely at about midlength of the sclerite (in *T. longiventris* and others); remainder of the sclerite not chitinized ..... 40

Ninth tergite of the male not chitinized, or else variously chitinized, either on the caudal margin, on the lateral margins, or with a conical tooth on the dorsal surface — in which case (*T. balioptera*) the cephalic and lateral margins are heavily chitinized and toothed ..... 41

40. Antennae bicolorous, the basal swelling of the flagellar segments black, the pedicels yellow; prescutum fawn-colored, with four light gray stripes partly margined with dark brown; prescutal interspaces with abundant brown dots; lateral margins of the abdominal segments broadly pale grayish silvery; male hypopygium with the ninth tergite (Plate L, 285) having the lateral lobes rounded, the median caudal notch indistinct. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate XLVI, 229, wing.)
*T. longiventris* Loew

Antennae unicolorous, the flagellar segments nearly uniform thruout; prescutum dull gray, with four dark brown stripes; lateral margins of the abdominal segments narrowly silvery; male hypopygium with the ninth tergite (Plate L, 286) having a deep U-shaped notch on the caudal margin. [Can. Ent., vol. 48, p. 46–48. 1916.]
*T. caroliniana* Alex.

41. Ninth tergite small, the caudal margin evenly rounded by a broad concavity which is very heavily chitinized; flagellar segments of antennae very deeply incised beneath, producing a serrated appearance ..... 42

Ninth tergite not as above ..... 43

42. Coloration bluish gray, including the abdomen; ninth tergite (Plate L, 284) with the caudal margin bluntly toothed. [Ross's Voyage to the Arctic Regions, p. 77, pl. A, fig. 15. 1831.] ..... *T. arctica* Curt.

Coloration brown, the abdomen dull brownish yellow with an interrupted dorsal stripe; ninth tergite (Plate L, 283) short and broad, the caudal margin heavily chitinized, deeply concave, and slightly roughened in places, the lateral angles produced into conspicuous chitinized points. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate LIV, 338, lateral aspect of male hypopygium.) ..... *T. septentrionalis* Loew

43. Ninth tergite (Plate L, 280) small, heavily chitinized, shiny black, the caudal margin with a deep U-shaped notch, a second tooth on either side, subbasal in position; wing of male 17.5 mm.; head light gray, with a narrow, impressed median line; antennae with the first three flagellar segments indistinctly bicolorous, the remainder uniformly dark brown; abdomen orange, with an interrupted dorso-median stripe. [Berl. Ent. Ztschr., vol. 8, p. 60. 1864.] (Plate LIV, 339, lateral aspect of male hypopygium.) *T. centralis* Loew

Ninth tergite larger, not as above ..... 44

44. Ninth tergite (Plate L, 279) heavily chitinized, black, hollowed out in a shallow saucer, the dorsal surface near the caudal margin with a prominent median tooth that is directed backward; margin of the saucer denticulate, more strongly behind; wing 16.8 mm.; head light gray; thorax dull gray, the prescutal stripes margined with brown. [Berl. Ent. Ztschr., vol. 7, p. 284. 1863.] (Plate XLVI, 227, wing; Plate LIV, 337, lateral aspect of male hypopygium.) ..... *T. balioptera* Loew

Ninth tergite not as above ..... 45

45. Ninth tergite (Plate L, 282) very large and extensive, narrowed slightly toward the apex, which consists of a flattened yellowish margin bearing a deep tho small median notch, the broad adjacent lobes with about three tiny teeth, the outermost one the largest; the part of the tergite behind the yellow caudal margin elevated, black, and including the basal two-thirds of the segment; wing 15 mm.; antennae blackish; prescutum light grayish brown, with about five dark brown stripes; abdominal segments dark brownish black, the caudal margin of each segment bright yellow, the lateral margins broadly gray; wings with a heavy pattern; a conspicuous dark spot at the base of the wing. [Berl. Ent. Ztschr., vol. 8, p. 57. 1864.] .... *T. ternaria* Loew

Ninth tergite not as above ..... 46

46. Ninth tergite (Plate L, 281) telescoped beneath segments 7 and 8; the sclerite not chitinized, very broad and short, the caudal margin broadly concave and provided with a uniform fringe of long yellow hairs; wing 15.7 mm.; antennae somewhat bicolorous, the basal enlargement of the flagellar segments dark brown, the remainder of each segment a little paler; prescutum whitish gray, with broad dull gray stripes narrowly and indistinctly margined with brown; abdomen dull yellow, with an indistinct dorso-median stripe which broadens out on segments 6 to 8; less distinct submarginal stripes on the sides of the abdomen. [Berl. Ent. Ztschr., vol. 8, p. 59. 1864.] (Plate LIV, 341, lateral aspect of male hypopygium.) ..... *T. canadensis* Loew

Ninth tergite not as above ..... 47

47. Ninth tergite (Plate L, 276) large, pale, not chitinized, with two rounded lobes separated by a narrow, deep notch; antennae elongate, the segments of the flagellum not incised beneath; ventro-caudal angle of each pleurite bearing a prominent, pale, fleshy lobe. [Berl. Ent. Ztschr., vol. 7, p. 286. 1863.] (Plate XLV, 212, wing.) *T. angustipennis* Loew

Ninth tergite not as above, more or less chitinized caudally; antennae shorter, the flagellar segments deeply incised beneath ..... 48

48. Ninth tergite (Plate L, 277) with a broad median chitinized tooth on the caudal margin; adjacent lateral lobes terminating in small, acute, chitinized points; antennae moderate in length, extending slightly beyond the wing root; prescutum fawn-colored, with four broad grayish brown stripes narrowly margined with brown; abdomen dull yellow with a rather indistinct brownish median stripe which is clearer behind. [Berl. Ent. Ztschr., vol. 7, p. 283. 1863.] ..... *T. serta* Loew

Ninth tergite (Plate L, 278) with a very broad, pale, median lobe; adjacent lateral lobes very prominent, directed caudad and slightly inward, the tips truncated and chitinized; coloration pale, yellowish, the lateral prescutal stripes and the scutal lobes grayish; the median prescutal stripe paler, more brownish; abdomen without distinct darker stripes; wing pattern pale. [*T. senega* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. pallida* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 284, 1863.] (Plate XLV, 213, wing.) ..... *T. senega* Alex.

49. Wing pattern dark brown sparsely marked with white, the dark brown including the wing apex and the anal and cubital cells, the white as a broad band before the cord and a blotch beyond the stigma; antennae bicolorous; prescutum with four stripes, the middle pair bifid at the anterior end; abdomen with three broad brown stripes; femora broadly tipped with dark brown (*fuliginosa* group). [*Ctenophora fuliginosa* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLVIII, 246, wing of female.) ..... *T. fuliginosa* (Say)

Wing pattern paler, brown or gray with the white more extensive ..... 50

50. Only the tergal valves of the female ovipositor present, these lying transversely conspicuously serrated along their outer edge (*arctica* group) ..... 51

All four valves of the ovipositor present, not serrated along their outer edge ..... 54

51. Abdomen gray or brownish gray ..... 52

Abdomen orange or orange-yellow on the basal tergites ..... 53

52. Coloration blue-gray; wing pattern pale, the brown and gray markings diffuse and ill-defined; length 24 mm. [Ross's Voyage to the Arctic Regions, p. 77, pl. A, fig. 15. 1831.] ..... *T. arctica* Curt.

Coloration light gray, the abdomen grayish brown with three indistinct brown stripes; wing pattern heavy, tessellated white and brown; antennae dark brown; head dark gray with a narrow brown median line; prescutum with three broad gray stripes margined with brown; length 27 mm. [*T. labradorica* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. tesselata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 277, 1863.] (Plate XLVI, 228, wing.) ..... *T. labradorica* Alex.

53. Abdomen very elongated; length of female over 30 mm.; antennae bicolorous; thoracic interspaces with tiny blackish dots. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate XLVI, 229, wing.) ..... *T. longiventris* Loew

Abdomen short, normal; length of female 25 mm.; wing pattern pale. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] ..... *T. serrulata* Loew

54. Large species, wing over 22 mm. (*valida* group). [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] ..... *T. valida* Loew

[Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.] ..... *T. hircuta* Doane

Smaller, wing under 20 mm. ..... 55

55. Wings gray, the apex darker; a broad white obliterative streak before the cord extending into the base of cell $M_4$; a brown spot at the origin of *Rs*; antennae bicolorous; shiny basal plate of the dorsal tergal valves of the ovipositor very elongate, as long as the valves themselves and longer than the seventh and eighth tergites taken together. [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) ... *T. submaculata* Loew

Wings not so colored ..... 56

56. Wings light gray, with a dark brown oval stigma and a broad grayish brown crossband extending from *Rs* across the wing; antennae bicolorous, at least basally; thoracic pleura with two longitudinal brown stripes. [*T. hermannia* Alex., Proc. Acad. Nat. Sci. Phila., p. 480, 1915. *T. fasciata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 279, 1863.] (Plate XLV, 211, wing.) ..... *T. hermannia* Alex.

Wings not so colored ..... 57

57. Wings grayish subhyaline, the apex narrowly and irregularly dark brown, the cord seamed with dark grayish brown; antennae dark brown thruout; thorax light gray, with four dark gray stripes which are margined with dark brown; thoracic pleura clear light gray, dorso-pleural membrane yellowish. [*T. iroquois* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. cincta* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 288, 1863.] (Plate XLVIII, 252, wing.) ..... *T. iroquois* Alex.

Wings not so colored ..... 58

58. Wings with about four large dark brown blotches along the radial vein, the second at the origin of the sector, the third at the stigma; wing apex narrowly light brown; wing about 16.5 mm.; antennae bicolorous; head dark gray, with a narrow, impressed, median line; prescutum dull gray with four clearly defined bright brown stripes; abdomen dull yellow with three dark brown stripes; tergal valves of ovipositor acicular. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] (Plate XLVII, 233, wing.)
*T. macrolabis* Loew

Wings not so colored....59

59. Thorax with the prescutal stripes concolorous with the ground color of the thorax, the lateral stripes broadly margined in front and on the sides with dark brown; median stripe broadly margined on the sides; wings with a variegated brown, gray, and white pattern (*hebes* group)....60

Thorax not so colored....62

60. Antennae bicolorous, at least basally. [Berl. Ent. Ztschr., vol. 7, p. 285. 1863.] (Plate XLVIII, 249, wing.)....*T. hebes* Loew

Antennae unicolorous....61

61. Cell $R_5$ of wings usually white or largely so; antennae shorter. [Berl. Ent. Ztschr., vol. 7, p. 281. 1863.]....*T. grata* Loew

Cell $R_5$ of wings infuscated except basally; antennae longer. [Berl. Ent. Ztschr, vol. 8, p. 60. 1864.]....*T. latipennis* Loew

62. Wings with a pale gray and hyaline pattern; cell *Sc* uniformly dark brown; *m-cu* cross-vein close to the fork of *M* (*marmorata* group)....63

Wings with the pattern darker gray and brown; if the pattern is pale, the cell *Sc* is not dark brown and the *m-cu* cross-vein is not close to the fork of *M* (*angustipennis* group)....64

63. Stripes on the prescutum ending at the level of the pseudosutural foveae, the median pair blunt at their anterior ends. [Berl. Ent. Ztschr., vol. 7, p. 279. 1863.] (Plate XLVIII, 250, wing.)....*T. fragilis* Loew

Median stripes of the prescutum extending about to the anterior margin of the sclerite, deeply bifid at their anterior ends. [Berl. Ent. Ztschr., vol. 7, p. 280. 1863.]
*T. ignobilis* Loew

64. Abdominal tergites dark slate gray, narrowly margined caudally with bright orange-yellow; length 24 mm.; wing 18 mm.; antennae dark brownish black thruout; head dark gray with a narrow brown median stripe; prescutum brownish gray, the stripes darker brown, not clear-cut; thoracic pleura clear gray; wing pattern heavy; a distinct dark brown spot at the base of the wing. [Berl. Ent. Ztschr., vol. 8, p. 57. 1864.]
*T. ternaria* Loew

Coloration not as above....65

65. Valves of ovipositor short, about as long as the fifth tergite. [*T. senega* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. pallida* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 284, 1863.] (Plate XLV, 213, wing.)....*T. senega* Alex.

Valves of ovipositor elongate, acicular, much longer than the fifth tergite alone....66

66. Abdomen orange, with three dark brownish black stripes; no basal gray ring on the abdominal tergites. [Berl. Ent. Ztschr., vol. 7, p. 286. 1863.] (Plate XLV, 212, wing.)....*T. angustipennis* Loew

Abdomen not so colored; a narrow basal ring on the abdominal tergites, grayish and destitute of the scattered hairs found on the remainder of the segment....67

67. Abdomen long and slender, indistinctly trivittate with brown, the stripes interrupted by the smooth basal areas of the segments. [Berl. Ent. Ztschr., vol. 7, p. 283. 1863.]
*T. serta* Loew

Abdomen with the lateral stripes broad, continuous; lateral margins of the segments broadly pale grayish. [*T. ignota* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. discolor* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 282, 1863.]
*T. ignota* Alex.

68. Cell *1st* $M_2$ open by the atrophy of the medial cross-vein; wing of female 10.5 mm.; coloration grayish brown, the thoracic stripes indistinct. [*Tipula aperta* Alex., Can. Ent., vol. 50, p. 62, 1918. *T. imperfecta* Alex., preoccupied, Proc. Acad. Nat. Sci. Phila., p. 484–485, pl. 16, fig. 9, 1915.] (Plate XLVII, 235, wing.) . . . *T. aperta* Alex.
Cell *1st* $M_2$ closed . . . . . 69
69. Color of wings almost uniformly dark brown (females only) . . . . . 70
Color of wings hyaline, pale grayish, or yellowish . . . . . 71
70. Size small, wing of female about 8 mm.; abdominal tergites uniformly dark brown thruout; cell *1st* $M_2$ pointed at its outer end, due to the extreme shortening of the medial cross-vein. [Journ. Acad. Nat. Sci. Phila., vol. 6, p. 151. 1829.] . . . . . *T. annulicornis* Say
Size larger, wing of female over 10 mm.; abdominal tergites dark brown, with broad, bright yellow, median triangles, the points directed forward; cell *1st* $M_2$ not pointed at its distal end, the medial cross-vein of normal length, nearly as long as the petiole of cell $M_1$. [Proc. Acad. Nat. Sci. Phila., p. 476–479, pl. 16, figs. 7, 8. 1915.] (Plate XLVIII, 244, wing.) . . . . . *T. taughannock* Alex.
71. Color of thorax light gray or blue-gray, with distinct clear-cut brown or black stripes; body clothed with long, pale hair; wing over 14 mm. Northern species . . . . . 72
Color of thorax brown, yellow, or gray; if grayish (*T. dejecta*), the wing is under 12 mm. and the body is not clothed with long, pale hair . . . . . 73
72. Color of thorax dull light gray, with four light brown stripes; median vitta of the head indistinct; dorsal abdominal vitta narrow; eighth abdominal tergite of female with the margins flattened and conspicuously expanded; tergal valves of the ovipositor long, pale. [Proc. Acad. Nat. Sci. Phila., p. 482–484, pl. 21, fig. 85. 1915.]
*T. piliceps* Alex.
Color of thorax blue-gray, with the stripes almost black, broad, the median pair tending to become confluent; median vitta of the head distinct; dorsal abdominal vitta broader, more diffuse; eighth abdominal tergite of female with the margins not conspicuously expanded; tergal valves of the ovipositor smaller; wing pale gray, stigma dark brown; antennae black thruout; ninth tergite of male deeply notched medially, the adjacent lateral lobes broad, truncated, pale; outer pleural appendages broad, pale; wing of male 14 mm. [Proc. Boston Soc. Nat. Hist., vol. 19, p. 42. 1876.]
*T. besselsi* O. S.
73. Males (as known) . . . . . 74
Females (as known) . . . . . 103
74. Caudal margin of ninth tergite (Plate L, 288) with a compressed median lobe projecting caudad of the short lateral lobes; distal end of cell *1st* $M_2$ pointed, cross-vein *m* very short; size very small, wing of male under 8 mm.; antennae elongated, bicolorous; thoracic stripes indistinct. [Journ. Acad. Nat. Sci. Phila., vol. 6, p. 151. 1829.] (Plate XLVIII, 243, wing; Plate LIII, 335, lateral aspect of male hypopygium.)
*T. annulicornis* Say
Caudal margin of ninth tergite without a compressed median lobe projecting beyond the lateral lobes; distal end of cell *1st* $M_2$ not pointed; size larger, wing of male over 10 mm . . . . . 75
75. Sclerites of ninth segment fused into a nearly complete ring; caudal margin of the tergite truncate with a broad, depressed, median lobe or with two approximated slender, parallel lobes, one on either side of the median line . . . . . 76
Sclerites of ninth segment not fused, at least the tergite distinct; ninth tergite without median lobes on the caudal margin . . . . . 80
76. Ninth tergite with two slender, finger-like lobes on the caudal margin (*tephrocephala* group) . . . . . 77
Ninth tergite with a single broad median lobe or with two short blunt lobes on the caudal margin (*perlongipes* group) . . . . . 78
77. Antennal flagellar segments bicolorous, the basal swelling of each segment yellow, the pedicel dark. [Berl. Ent. Ztschr., vol. 8, p. 62. 1864.] (Plate XLVI, 221, wing; Plate XLIX, 271, ninth tergite.) . . . . . *T. tephrocephala* Loew

Antennal flagellar segments bicolorous, the basal swelling of each segment black, the pedicel yellow. [Proc. Acad. Nat. Sci. Phila., p. 485–487, pl. 16, fig. 10. 1915.] (Plate XLVI, 222, wing; Plate XLIX, 272, ninth tergite; Plate LIII, 325, eighth sternite.) ..... *T. cayuga* Alex.

78. Size small, wing 12 mm.; thoracic dorsum dull gray, with four brownish stripes; antennae unicolorous, dark brown; pleura clear light gray; sides of postnotum light yellow; ninth tergite (Plate XLIX, 270) with two broad lobes, the notch between deep. [Journ. N. Y. Ent. Soc., vol. 9, fig. 99. 1901.] (Plate XLVI, 225, wing.)
*T. sulphurea* Doane

Size larger, wing 14 mm. or over; thoracic dorsum not colored as above ..... 79

79. Antennae bicolorous; thoracic dorsum dull yellow with three brown stripes, the lateral pair less distinct than the median one; legs long; male hypopygium with the median lobe of the ninth tergite (Plate XLIX, 268) entire or the bifid nature barely indicated. [*T. perlongipes* Johns., Proc. Boston Soc. Nat. Hist., vol. 34, p. 131, 1909. *T. filipes* Walk., preoccupied, List Dipt. Brit. Mus., p. 65, 1848.] (Plate XLVI, 223, wing.) ..... *T. perlongipes* Johns.

Antennae unicolorous or nearly so; thorax gray, with three broad, more or less distinct, stripes, the median one with a delicate dark brown line; legs short; male hypopygium with the median lobe of the ninth tergite (Plate XLIX, 269) bifid. [Proc. Acad. Nat. Sci. Phila., p. 480–482, pl. 16, fig. 6. 1915.] (Plate XLVI, 224, wing; Plate LIII, 331, lateral aspect of male hypopygium.) ..... *T. kennicotti* Alex.

80. Ninth tergite (Plate LII, 309) large, the caudal margin with a small rounded notch on either side of a small acute median tooth; eighth sternite with broad, fleshy, lateral lobes directed proximad and with the ventral inner angle produced into a chitinized point and clothed with long yellow hairs; median area of the sternite with a prominent chitinized tooth on either side of the median line, broadly separated by a distance greater than the diameter of one tooth; size large, wing 18–20 mm.; antennae bicolorous. [Berl. Ent. Ztschr., vol. 7, p. 292. 1863.] (Plate XLVII, 236, wing.)
*T. umbrosa* Loew

Ninth tergite not as described; eighth sternite, if with fleshy lateral lobes (*T. australis*, *T. valida*, and others), without two chitinized teeth on the caudal margin of the sternite ..... 81

81. Size large, wing over 20 mm.; male hypopygium greatly enlarged; eighth sternite with elongate lateral lobes and a flattened median lobe (*valida* group; included also in the section with marked wings, because the tips of the wings are usually of a darker gray than the basal part) ..... 82

Size smaller, wing under 18 mm.; male hypopygium not greatly enlarged; eighth sternite not as above ..... 83

82. Ninth tergite (Plate LI, 303) with the lateral lobes more slender and pronounced; eighth sternite without a long brush of hairs. [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] (Plate XLVII, 237, wing.) ..... *T. valida* Loew

Ninth tergite (Plate LI, 304) with the lateral lobes shorter and blunter; eighth sternite with a brush of long yellow hairs. [Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.]
*T. hirsuta* Doane

83. Wing apex a little grayer than the basal cells of the wings; a brown spot at the origin of the sector; male hypopygium with the ninth tergite (Plate LII, 317) large, deeply split by a broad V-shaped notch, the lateral lobes acutely pointed. (This species is included also in the section with marked wings, because the tips of the wings are usually of a darker gray than the basal part.) [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) ..... *T. submaculata* Loew

Wing apex unicolorous or nearly so; ninth tergite not as described ..... 84

84. Antennae unusually elongated, if bent backward extending to the base of the fifth abdominal segment; ninth tergite (Plate LI, 290) with the lateral lobes subacute, the median lobe situated in a deep, shield-shaped depression; eighth sternite unarmed; antennae unicolorous; abdominal tergites bright yellow, with three distinct brownish

black stripes which are confluent across the bases and less distinctly across the apices of tergites 2 to 5; wing 15 mm.; cell *1st* $M_2$ elongate; wings yellowish subhyaline, the obliterative streak very reduced, appearing as a spot before the stigma and a linear dash in the base of cell *1st* $M_2$ and the end of cell *R*. [Proc. Acad. Nat. Sci. Phila., p. 476 479, pl. 16, figs. 7, 8. 1915.] (Plate LIII, 336, lateral aspect of male hypopygium.) ..... *T. taughannock* Alex.

Antennae shorter, not extending beyond the base of the abdomen; ninth tergite not as described; if at all similar (*T. monticola*), the eighth sternite armed with brushes of hairs or bristles ..... 85

85. Ninth tergite (Plate LI, 301) small, with the caudal margin bearing a blunt median lobe and with a prominent divergent horn on either side; thoracic pleura clear light gray; eighth sternite unarmed; size small, wing 11.5 mm.; antennae uniform dark brown. [Ins. Saunders., vol. 1, Dipt., p. 442. 1856.] (Plate XLVIII, 251, wing.) *T. dejecta* Walk.

Ninth tergite not as above ..... 86

86. Ninth tergite (Plate LII, 308) small, the caudal margin with a broad V-shaped notch; ninth pleurite produced caudad into a short, flattened, subspatulate lobe; eighth sternite extensive, narrowed behind, the caudal margin broadly U-shaped and bearing a row of prominent yellow hairs; color light gray, the thorax marked with brown; wing about 16 mm. [Proc. Acad. Nat. Sci. Phila., p. 488–490, pl. 16, fig. 12. 1915.] (Plate XLVII, 234, wing.) ..... *T. loewiana* Alex.

Hypopygial characters not as above ..... 87

87. Coloration of thoracic pleura light gray; thoracic dorsum gray or grayish, with brown stripes ..... 88

Coloration of thoracic pleura yellow, in some cases whitish pollinose; dorsum yellow or brown ..... 90

88. Ninth sternite with a stout pendulous lobe directed ventrad, bearing a dense tuft or pencil of long reddish hairs; eighth sternite large, prominent, extending far caudad and its concavity forming a sheath for the base of the ninth sternite, the lateral angles bearing dense tufts of long, reddish-silvery hairs which are decussate; between these lobes a broad median projection, the lateral angles of which are slightly recurved and the caudal margin is broadly concave; color grayish, with distinct dark brown thoracic stripes; wings light brown, the tips a little darker; a large vitreous spot before and beyond the stigma; wing of male 12.6 mm. Arctic species. [Proc. Acad. Nat. Sci. Phila., p. 496-497. 1915.] (Plate LII, 314, ninth tergite.) ... *T. penicillata* Alex.

Hypopygial characters not as above. Austral species ..... 89

89. Antennae short, the flagellar segments deeply constricted beyond the basal enlargement; six brown stripes on the mesonotal prescutum; male hypopygium with the ninth tergite (Plate LII, 305) almost straight across the caudal margin, with a deep and narrow impressed median furrow; lobes of the caudo-lateral angles of the ninth sternite pendulous, directed ventrad, the apices clothed with short golden hairs; eighth sternite (Plate LIII, 326) with four conspicuous lobes, the outer pair very broad and flattened, their apices oblique, the inner pair being the divaricate ends of a median process on the caudal margin of the sternite, their apices clothed with a dense brush of golden-yellow hair. [Journ. N. Y. Ent. Soc., vol. 9, p. 104–105. 1901.] ... *T. australis* Doane

Antennae longer, the flagellar segments not constricted beyond the basal enlargement; three brown stripes on the mesonotal prescutum; male hypopygium with the ninth tergite (Plate LII, 306) having the caudal margin deeply and broadly notched medially; lobes of the caudo-lateral angles of the ninth sternite not pendulous, directed inward; eighth sternite (Plate LIII, 327) without lobes on the caudal margin. [Proc. Acad. Nat. Sci. Phila., p. 501-504, pl. 17, fig. 19. 1915.] (Plate XLVII, 238, wing.) *T. dietziana* Alex.

90. Coloration bright brownish yellow, the thorax with dark brown stripes; pleura dull yellow, whitish pollinose; male hypopygium with the ninth tergite (Plate LII, 307) broadly concave caudally, the lateral angles not prominent; antennae with the three

basal segments light yellow, the remainder of the organ more or less distinctly bicolorous; abdomen dull yellow, the tergites with a conspicuous dark brown stripe; wing 12 mm. [Proc. Acad. Nat. Sci. Phila., p. 475–476, pl. 16, fig. 5. 1915.] (Plate XLVIII, 253, wing; Plate LIV, 346, lateral aspect of male hypopygium.) ..... *T. mainensis* Alex.

Coloration not as above, the thoracic stripes not dark brown; hypopygium not as above ..... 91

91. Nasus short; cell *1st* $M_2$ of wings very small and pentagonal; male hypopygium with the ninth tergite usually tumid, unarmed or provided with horns; in species in which the tergite is not conspicuously swollen and tumid (*T. parshleyi*), the cell *1st* $M_2$ is small and pentagonal, as above; in species in which the cell *1st* $M_2$ is longer (*T. johnsoniana*), the ninth tergite is tumid tho unarmed (*bicornis* group) ..... 92

Nasus usually longer; cell *1st* $M_2$ of wings not small and pentagonal; male hypopygium with the ninth tergite not tumid (*translucida* group) ..... 96

92. Ninth tergite (Plate LII, 321) not tumid; eighth sternite very long, sheathing the ninth sternite beneath, the tip with two chitinized points on either side. [Proc. Acad. Nat. Sci. Phila., p. 510–512, pl. 17, fig. 23. 1915.] (Plate LV, 354, lateral aspect of male hypopygium.) ..... *T. parshleyi* Alex.

Ninth tergite tumid; eighth sternite shorter, not closely applied to ninth sternite for the entire length of the latter, the apex without chitinized points ..... 93

93. Ninth tergite (Plate LII, 320) with four lobes or horns. [Journ. N. Y. Ent. Soc., vol. 9, p. 112–113. 1901.] (Plate XLVI, 231, wing; Plate LV, 353, lateral aspect of male hypopygium.) ..... *T. megaura* Doane

Ninth tergite with two horns or without horns ..... 94

94. No horns on the tergite (Plate LII, 318). [Proc. Acad. Nat. Sci. Phila., p. 505–506, pl. 17, fig. 20. 1915.] (Plate LV, 351, lateral aspect of male hypopygium.) *T. johnsoniana* Alex.

Horns on the tergite ..... 95

95. Horns on tergite (Plate LII, 319) directed upward. [16th Rept. State Ent. Ill., p. 78, pl. 6, fig. 4. 1891.] (Plate XLVI, 230, wing; Plate LV, 350, lateral aspect of male hypopygium.) ..... *T. bicornis* Forbes

Horns on tergite directed caudad or slightly ventrad. [Proc. Acad. Nat. Sci. Phila., p. 507–508, pl. 17, fig. 21. 1915.] (Plate LV, 352, lateral aspect of male hypopygium.) *T. morrisoni* Alex.

96. Caudal margin of ninth tergite (Plate LII, 315) with three prominent lobes, the median lobe acute; antennae bicolorous; body coloration light yellow, the thoracic stripes reddish brown; abdomen with a series of about four conspicuous, rounded, brown spots along the sides; wing 13.5 mm. Southern species. [Proc. Acad. Nat. Sci. Phila., p. 487–488, pl. 16, fig. 11. 1915.] (Plate XLVII, 240, wing.) ..... *T. triton* Alex.

Caudal margin of ninth tergite not trifid ..... 97

97. Caudal margin of ninth tergite (Plate LII, 316) deeply notched, the lateral lobes produced into long, slightly curved horns; outer pleural lobe a conspicuous curved hook; antennae bicolorous; body coloration yellowish, the thoracic stripes very indistinct; wings yellowish; wing 17.2 mm. [Proc. Acad. Nat. Sci. Phila., p. 493–495, pl. 16, fig. 15. 1915.] (Plate XLVII, 241, wing; Plate LIII, 328, eighth sternite; Plate LV, 349, lateral aspect of male hypopygium.) ..... *T. tuscarora* Alex.

Male hypopygium not as above ..... 98

98. Lateral lobes of ninth tergite (Plate LII, 310) broad, squarely truncated; antennae more or less distinctly bicolorous; coloration brownish yellow; wing 18 mm. [Proc. Acad. Nat. Sci. Phila., p. 490–492, pl. 16, fig. 13. 1915.] (Plate XLVII, 242, wing.) *T. mingwe* Alex.

Lateral lobes of ninth tergite not squarely truncated, more or less pointed or rounded ..... 99

99. Lateral lobes of ninth tergite pointed ..... 99

Lateral lobes of ninth tergite rounded ..... 100

100. Inner pleural appendage produced caudad into an elongate, subacute, pale, fleshy lobe ..... 101

Inner pleural appendage complex, consisting of a slender caudal lobe which is directed backward and pointed, and a cephalic lobe which is compressed, black, and heavily chitinized along the margin; coloration yellowish; antennae bicolorous; head light gray; thoracic stripes rather indistinct, brownish orange; ninth tergite (Plate LII, 312) with the lateral angles tipped with a cylindrical, conical point; median lobe prominent, convex, rounded; eighth sternite large, prominent, projecting caudad, the posterior margin with a rounded notch bearing a dense tuft of long, silvery hairs on each side of the mid-line; wing of male 18–19 mm. [Proc. Acad. Nat. Sci. Phila., p. 492–493, pl. 16, fig. 14. 1915.] (Plate LV, 347, lateral aspect of male hypopygium.) ..... *T. monticola* Alex.

101. Antennal flagellum dark brown; body coloration light gray; ninth tergite with the lateral angles subangular, not approximated; median lobe not prominent, shiny; thorax with three broad brown stripes; wing 12.5 mm. Southern species. [Insec. Inscit. Menst., vol. 3, p. 134–136. 1915.] ..... *T. catawba* Alex.

Antennal flagellum bicolorous; body coloration yellowish, the thoracic stripes indistinct; ninth tergite (Plate LII, 313) with the acute lateral lobes approximated, the space between narrow. [Journ. N. Y. Ent. Soc., vol. 9, p. 109. 1901.] *T. translucida* Doane

102. Abdominal tergites 2 to 5 with a brown subbasal spot on the lateral margin; ninth tergite of male with a deep rectangular notch, the median area not convex; antennae indistinctly bicolorous; thorax brownish yellow without distinct stripes; wing 12.6 mm. Southern species. [Proc. Acad. Nat. Sci. Phila., p. 495–496, pl. 16, fig. 16. 1915.] (Plate LV, 348, lateral aspect of male hypopygium.) ..... *T. seminole* Alex.

Abdominal tergites without a brown subbasal spot on the lateral margin; ninth tergite of male (Plate LII, 311) with the lateral angles conspicuous, the apices bluntly rounded; median area broad, highly convex to obtusely pointed, shiny chestnut brown to yellow; antennae usually bicolorous; thorax light brownish yellow, the stripes a little darker, pale brown; wing about 13 mm. [Insec. Inscit. Menst., vol. 3, p. 134–135. 1915.] ..... *T. georgiana* Alex.

103. Lobes of ovipositor blunt, unchitinized ..... *bicornis* group

Lobes of ovipositor pointed, chitinized .... Females of other species with unmarked wings

No attempt is made here to separate the females of the species with unmarked wings; many of the species have not been definitely associated with their mates and are not really known. In all cases in which pairs of flies are taken in copula, the two sexes should be pinned on the same pin, the male above. In many groups of the genus it is quite impossible to separate the females on the characters known at present.

Since the above key was completed a few additional species of Tipula have been described. These are briefly diagnosed here in order to complete the data.

*Tipula aprilina* Alex. (Alexander, 1918 a: 63–64.)

*Dejecta* group; close to *T. dejecta*. Male hypopygium with the ninth tergite large, the posterior margin with the lateral angles produced caudad into prominent blunt lobes which are blackened and furnished with small tubercles, the caudal margin truncated; between these lateral lobes two parallel, usually longer and slightly pointed, lobes which are directed slightly ventrad, one on either side of the median line; outer pleural appendage very small and inconspicuous, elongate-cylindrical, yellowish; inner pleural appendage elongate, narrow; margins of ninth sternite not widely separated beneath, carinate, and with a narrow V-shaped posterior notch bearing a pair of small, fleshy lobes. Wing of male, 11.5 mm. (Virginia, April.)

*T. conspicua* Dietz. (Dietz, 1917:149–150.)
*Tricolor* group; close to *T. eluta*. Grayish white; antennal flagellum distinctly bicolorous; thoracic stripes margined with brown, the median stripe divided by a dark line; hyaline vitta of wings reaching the outer margin; abdomen yellow, unstriped; ninth tergite with lateral pencils of hairs. Wing of male, 17 mm. (North Carolina, September.)

*T. sackeniana* Alex. (Alexander, 1918 a:62–63.)
*Tricolor* group; close to *T. tricolor*. Coloration reddish brown; antennae bicolorous; male hypopygium without a pencil of hairs on either side of median lobe of tergite. Wing of male, 15.5 mm. (New York, Maryland, Virginia, and Georgia, July and September.)

*T. vicina* Dietz. (Dietz, 1917:148–149.)
*Tricolor* group; close to *T. eluta*. Grayish brown; antennal flagellum unicolorous brown; mesonotal stripes margined with brown, the median stripe divided by a blackish line; hyaline vitta of wings extending thru cells *1st* $M_2$ and $R_5$ to margin; abdomen striped laterally. Wing of male, 13 mm. (New York, May; Michigan, July.)

*T. entomophthorae* Alex. (Alexander, 1918 c:385–386.)
*Trivittata* group; close to *T. angulata*. Mesonotal prescutum gray with three brown stripes; wings gray with a broad white crossband beyond the cord; vein $R_2$ persistent for its entire length; male hypopygium with the ninth tergite deeply notched medially, the lateral angles obliquely truncated. Wing of male, 15.8 mm. (North Carolina.)

*T. flavibasis* Alex. (Alexander, 1918 c:411–412.)
*Valida* group. A small, pale brownish species, easily distinguished from all its relatives by the bicolorous antennae, the basal enlargements of the segments being light yellow and the remainder black. Antennae of male long and slender, if bent backward extending to beyond base of abdomen. In coloration of antennae the species in the faunal limits of this paper is approached only by *T. tephrocephala*, a very different fly. Wing of male, 12 mm. (Kansas, July.)

*T. huron* Alex. (Alexander, 1918 a:66–67.)
*Valida* group; close to *T. submaculata*. Wings with a heavy brown pattern resembling *T. trivittata* or *T. angulata*. Wing of male, 15.6 mm. (Wisconsin, June.)

*T. margarita* Alex. (Alexander, 1918 b:243–244.)
General coloration of head and thorax light gray; antennae short, black, the three basal segments orange-yellow; femora with a broad subterminal yellow ring, most distinct on the fore legs; wings with four brown crossbands; abdomen yellow, the tergites with a broad dark brown median stripe and narrow sublateral stripes, the lateral margin of the tergites broadly light gray; male hypopygium with the ninth tergite large, subquadrate, with a deep median split, the ninth pleurite complete, the eighth sternite with a large tuft of yellow hairs on either side of the median line. Wing of male, 14.4 mm. (New York, June.)

*T. fultonensis* Alex. (Alexander, 1918 a:67.)
*Arctica* group; close to *T. longiventris*. Abdomen of female about one-half inch shorter than in the female of *longiventris* (16 mm.). Wing of female, 18.5 mm. (New York, June.)

*T. helderbergensis* Alex. (Alexander, 1918 a:64–65.)
*Hebes* group; close to *T. latipennis*. General color very dark; antennal flagellum uniformly brown; male hypopygium with the eighth sternite densely fringed with long golden hairs. Wing of male, 14 mm. (New York, July.)

It will be noted that many names are not included in this key to the genus Tipula, and this is because most of them are synonymous with species that are included. The principal synonymy is as follows:

| | | |
|---|---|---|
| *T. apache* Alex. | = | *T. dorsolineata* Doane |
| *T. calva* Doane | = | *T. valida* Loew |
| *T. casta* Loew | = | *T. cunctans* Say |
| *T. cincta* Loew | = | *T. iroquois* Alex. |
| *T. costalis* Say | = | *T. sayi* Alex. |
| *T. cuspidata* Doane | = | *T. submaculata* Loew |
| *T. decora* Doane | = | *T. angulata* Loew |
| *T. discolor* Loew | = | *T. ignota* Alex. |
| *T. fasciata* Loew | = | *T. hermannia* Alex. |
| *T. filipes* Walk. | = | *T. perlongipes* Johns. |
| *T. flavicans* Fabr. | = | *T. ultima* Alex. |
| *T. fumosa* Doane | = | *T. dejecta* Walk. |
| *T. illinoiensis* Alex. (female) | = | *T. senega* Alex. (male) |
| *T. illustris* Doane | = | *Stygeropis fuscipennis* Loew |
| *T. imperfecta* Alex. | = | *T. aperta* Alex. |
| *T. inermis* Doane | = | *T. umbrosa* Loew |
| *T. infuscata* Loew | = | *T. cunctans* Say |
| *T. jejuna* Johns. (female) | = | *T. annulicornis* Say |
| *T. ottawaensis* Dietz | = | *T. latipennis* Loew |
| *T. pallida* Loew | = | *T. senega* Alex. |
| *T. speciosa* Loew (male) | = | *T. fuliginosa* (Say) |
| *T. spectabilis* Doane | = | *T. macrolabis* Loew |
| *T. suspecta* Dietz | = | *T. afflicta* Dietz |
| *T. suspecta* Loew | = | *T. fragilis* Loew |
| *T. tesselata* Loew | = | *T. labradorica* Alex. |
| *T. versicolor* Loew (female) | = | *T. senega* Alex. (female) |
| *T. winnemana* Alex. | = | *T. johnsoniana* Alex. |

In addition the following species, which are not recognizable from the descriptions, are omitted:

*T. borealis* Walk.
*T. duplex* Walk.
*T. maculipennis* Say
*T. platymera* Walk.
*T. puncticornis* Macq.
*T. resurgens* Walk.
*T. retorta* v. d. W.
*T. triplex* Walk.
*T. vitrea* v. d. W.

*T. albonotata* Doane is probably a good species, close to *T. trivittata* Say but with the thoracic pattern different, the prescutum with three broad brown stripes.

*T. cincticornis* Doane is likewise a good species, rather similar to *T. translucida* Doane (page 955) but with the outer pleural lobe longer and the pendulous appendage of the ninth sternite shorter. It differs from *T. monticola* Alex. (page 955) in the structure of the eighth sternite, the yellow head, the yellow thoracic pleura, and other characters.

*T. maculipennis* Say is probably *T. angustipennis* Loew but the spec is in doubt. Specimens in the Harris collection of the Boston Socie of Natural History are determined by Say, tho not of the original seri and these are *T. angustipennis* or close to it. However, the descripti of the species shows that it differs in several important respects from specimens of *T. angustipennis* that the writer has seen, and it seer that the species must for the present remain in doubt.

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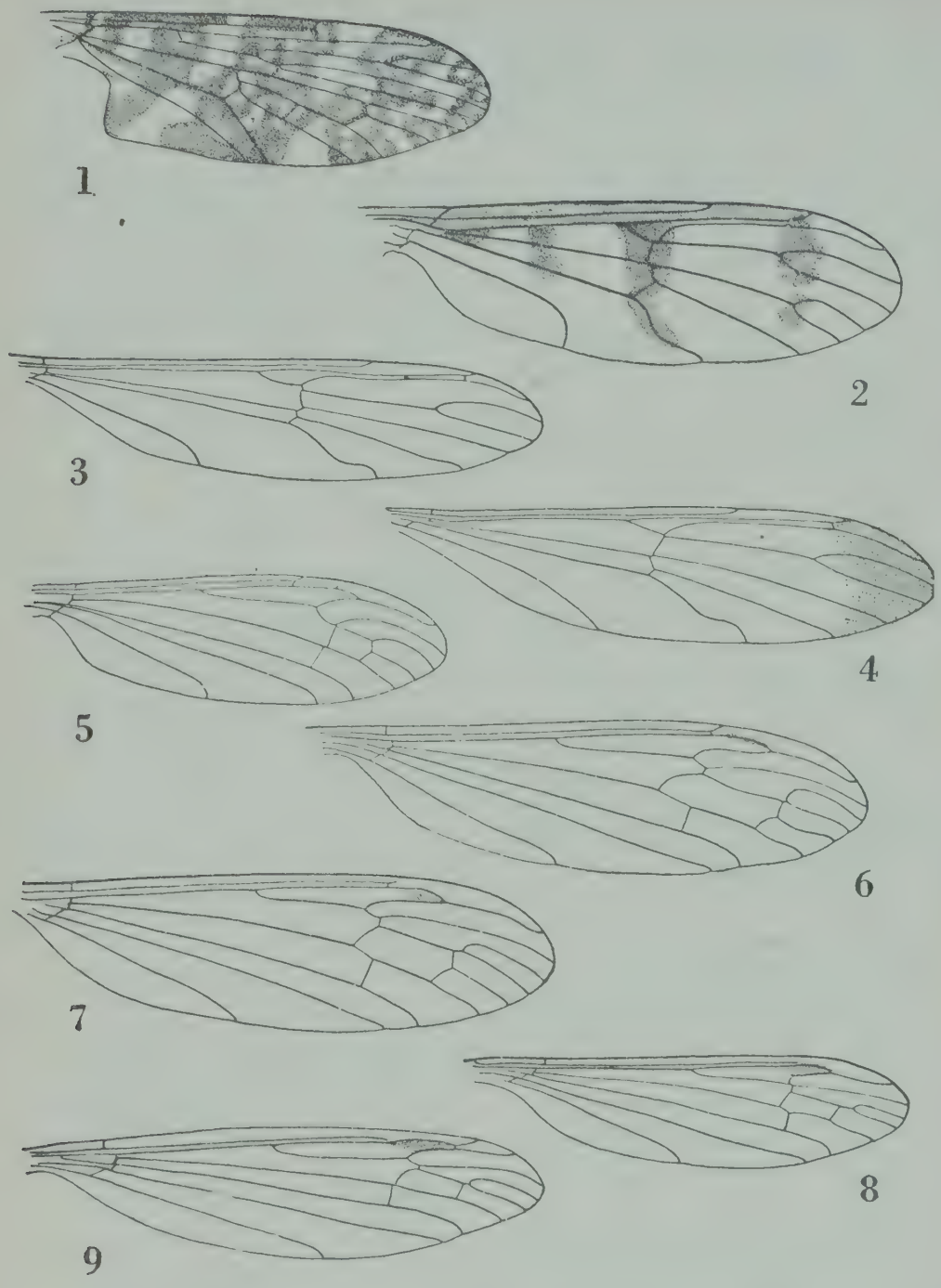
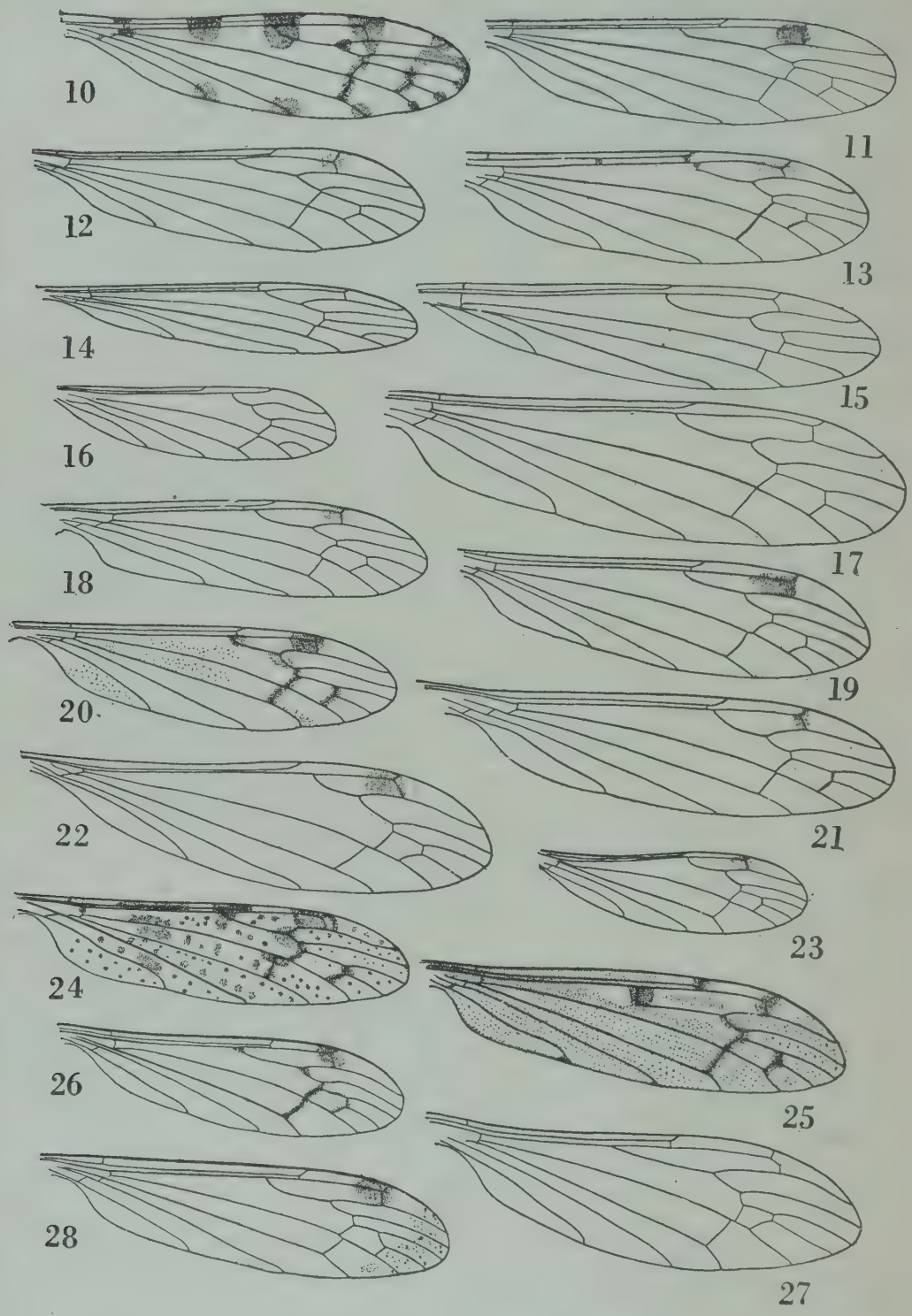



WINGS OF TANYDERIDAE, PTYCHOPTERIDAE, AND TIPULIDAE (CYLINDROTOMINAE)

1, *Protoplasa fitchii*
2, *Ptychoptera rufocincta.* 3, *Bittacomorpha clavipes.* 4, *Bittacomorphella jonesi*
5, *Liogma nodicornis.* 6, *Cylindrotoma americana*; 7, *C. tarsalis.* 8, *Phalacrocera tipulina*; 9, *P. neoxena*

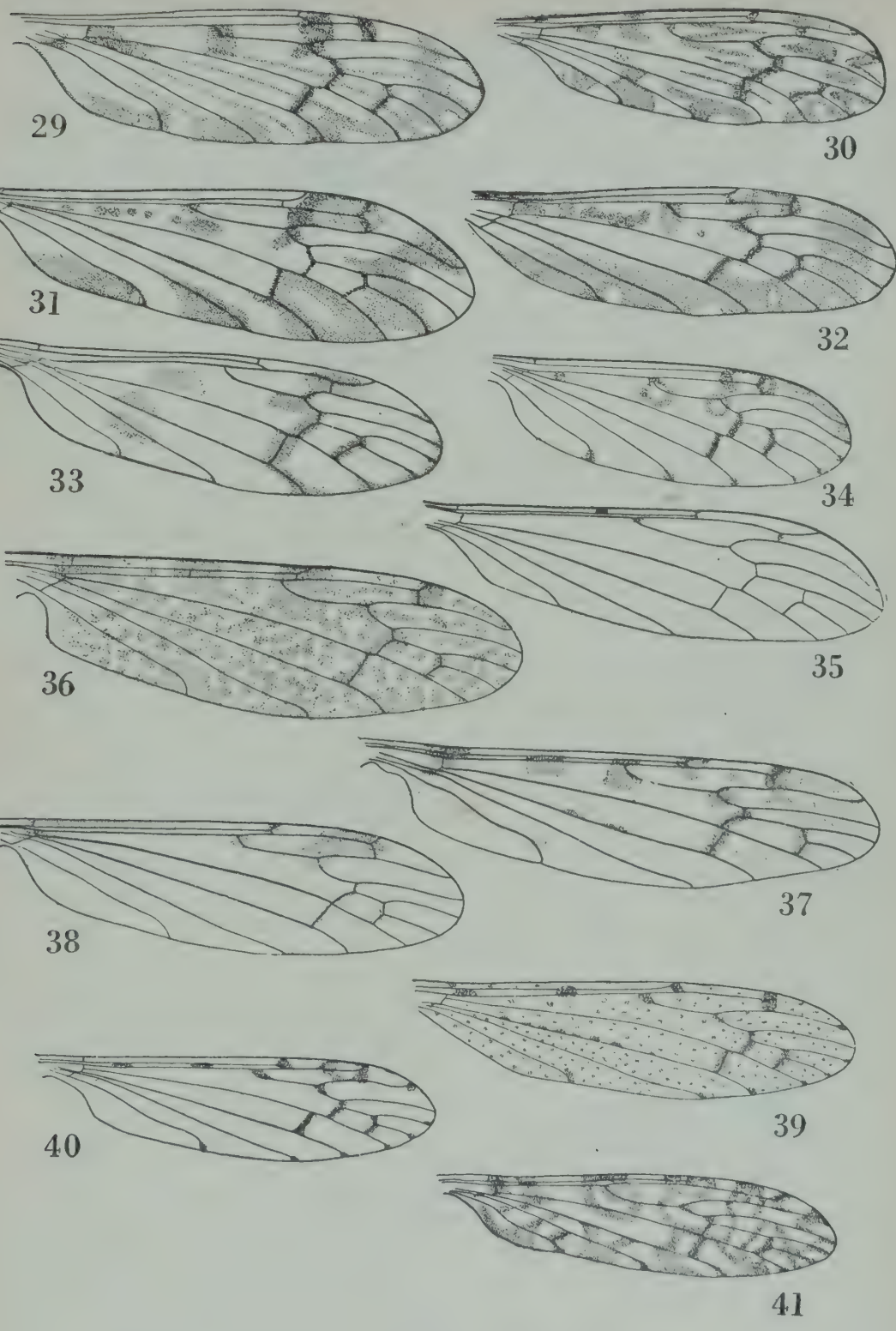
(963)




WINGS OF TIPULIDAE (LIMNOBIINI)

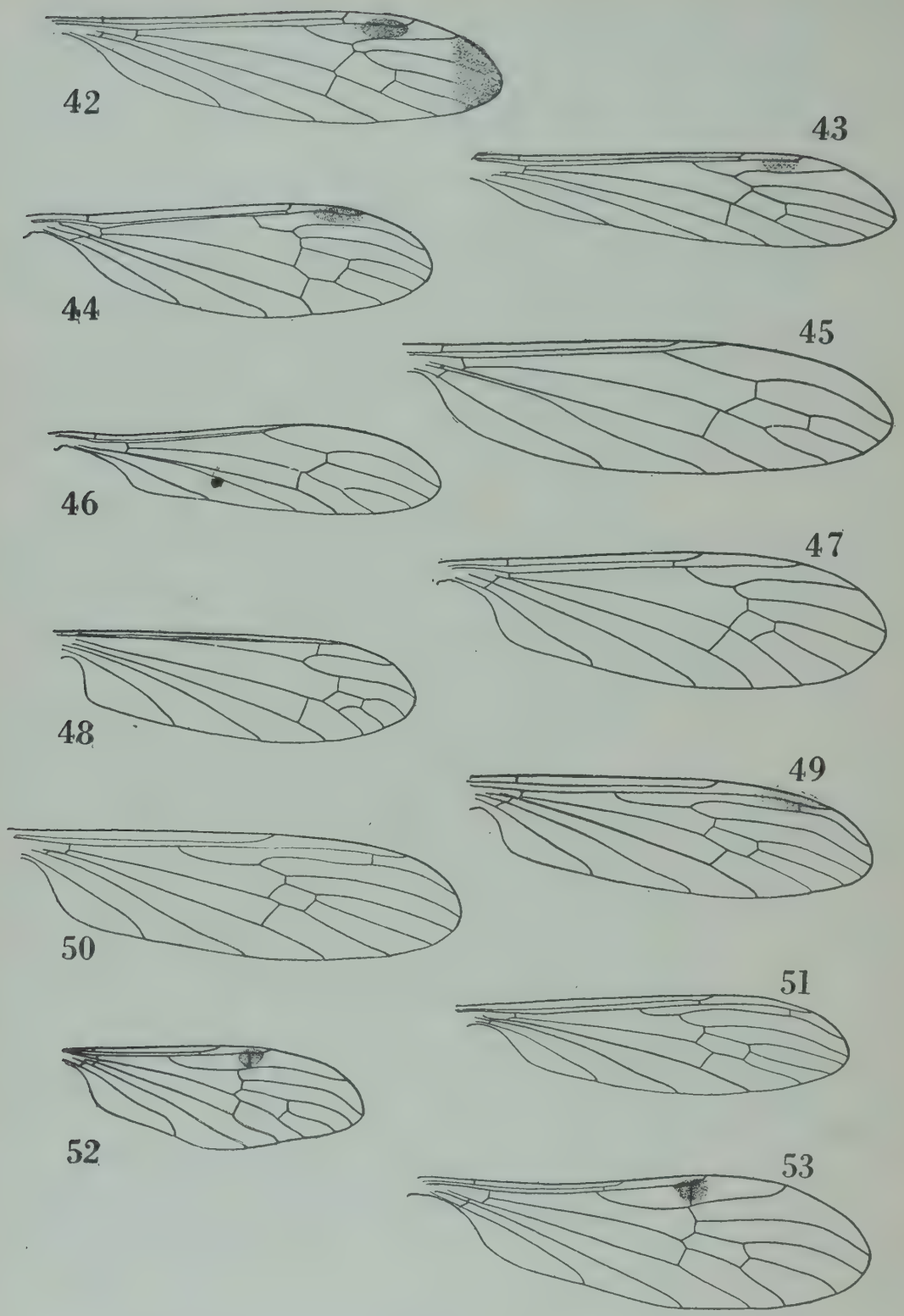
10, *Geranomyia rostrata*. 11, *G. canadensis*. 12, *G. distincta*. 13, *G. diversa* 14, *Dicranomyia longipennis*. 15, *D. whartoni*. 16, *D. rostrifera*. 17, *D. haeretica*. 18, *D. halterata*. 19, *D. monticola*. 20, *D. badia*. 21, *D. liberta*. 22, *D. pudica*. 23, *D. morioides*. 24, *D. simulans*. 25, *D. rara*. 26, *D. macateei*. 27, *D. globithorax*. 28, *D. pubipennis*

(964)



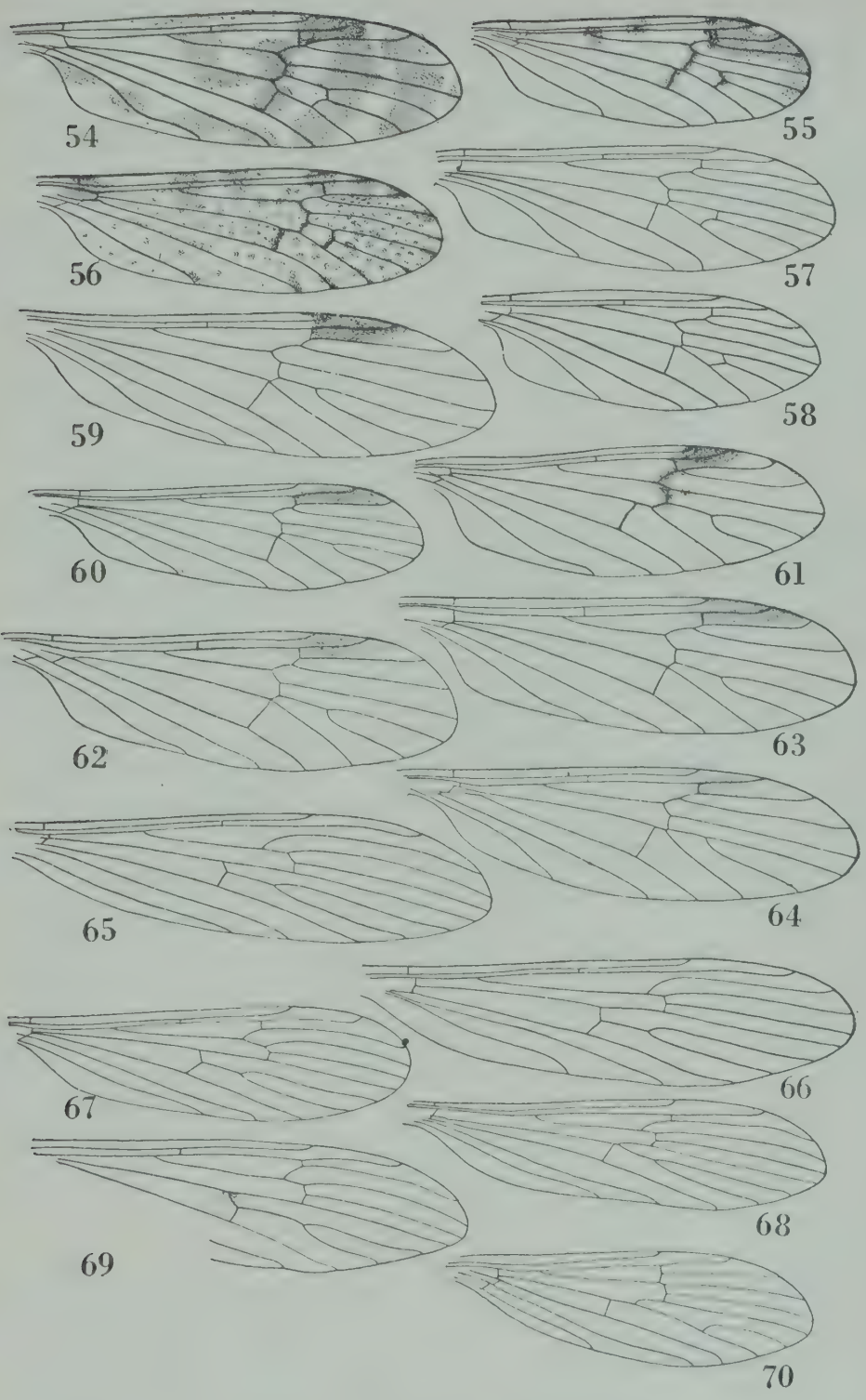

WINGS OF TIPULIDAE (LIMNOBIINI)

29, *Limnobia cinctipes*. 30, *L. parietina*. 31, *L. solitaria*. 32, *L. fallax*. 33, *L. indigena*. 34, *L. triocellata*. 35, *L. tristigma*
36, *Rhipidia maculata*. 37, *R. bryanti*. 38, *R. fidelis*. 39, *R. shannoni*. 40, *R. domestica*
41, *Discobola argus*



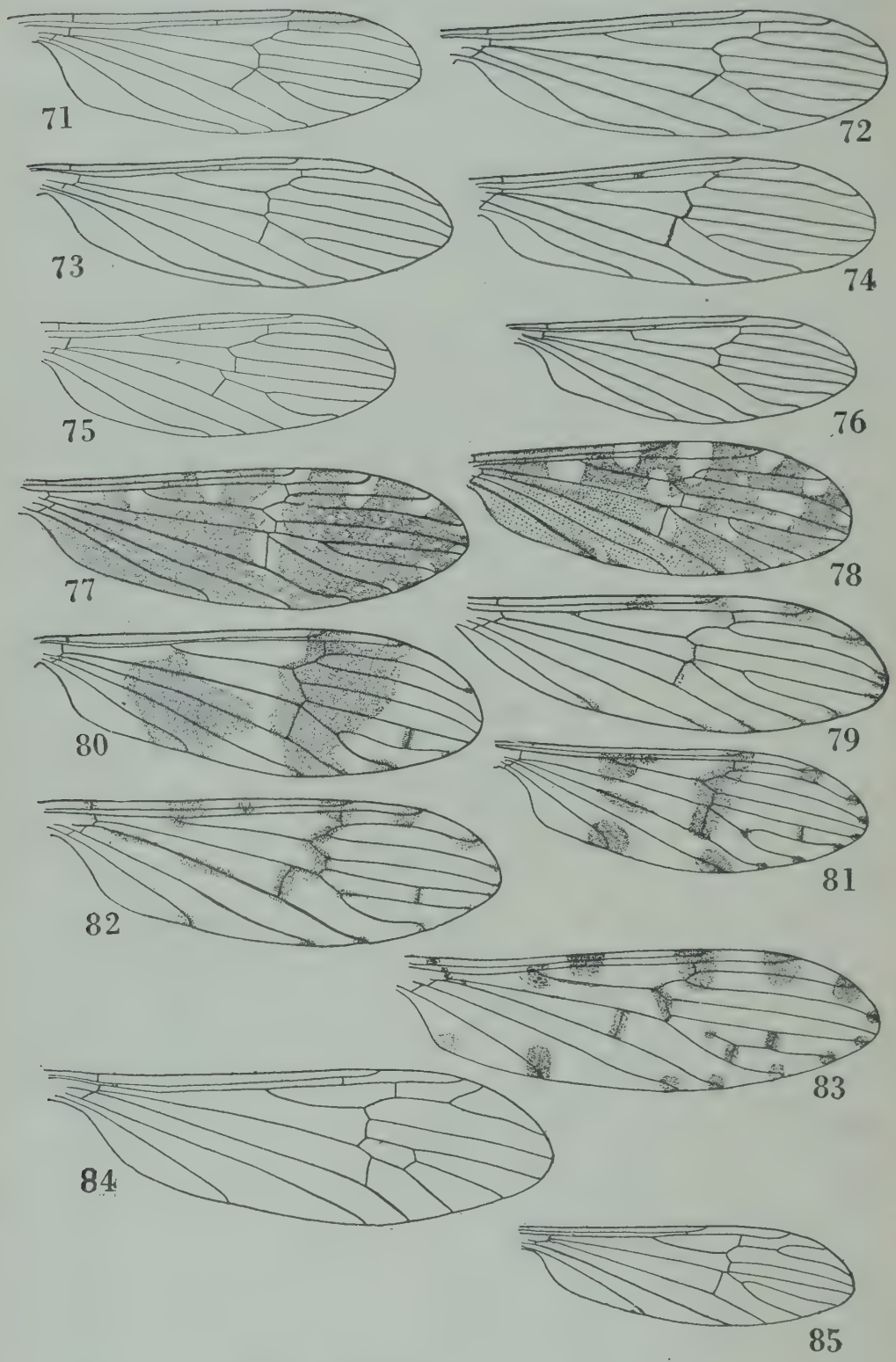

WINGS OF TIPULIDAE (ANTOCHINI)

42, *Rhamphidia flavipes*; 43, *R. mainensis*. 44, *Elephantomyia westwoodi*. 45, *Toxorhina magna*; 46, *T. muliebris*. 47, *Atarba picticornis*. 48, *Antocha saxicola*. 49, *Dicranoptycha germana*; 50, *D. winnemana*; 51, *D. sobrina*. 52, *Teucholabis complexa*; 53, *T. lucida*



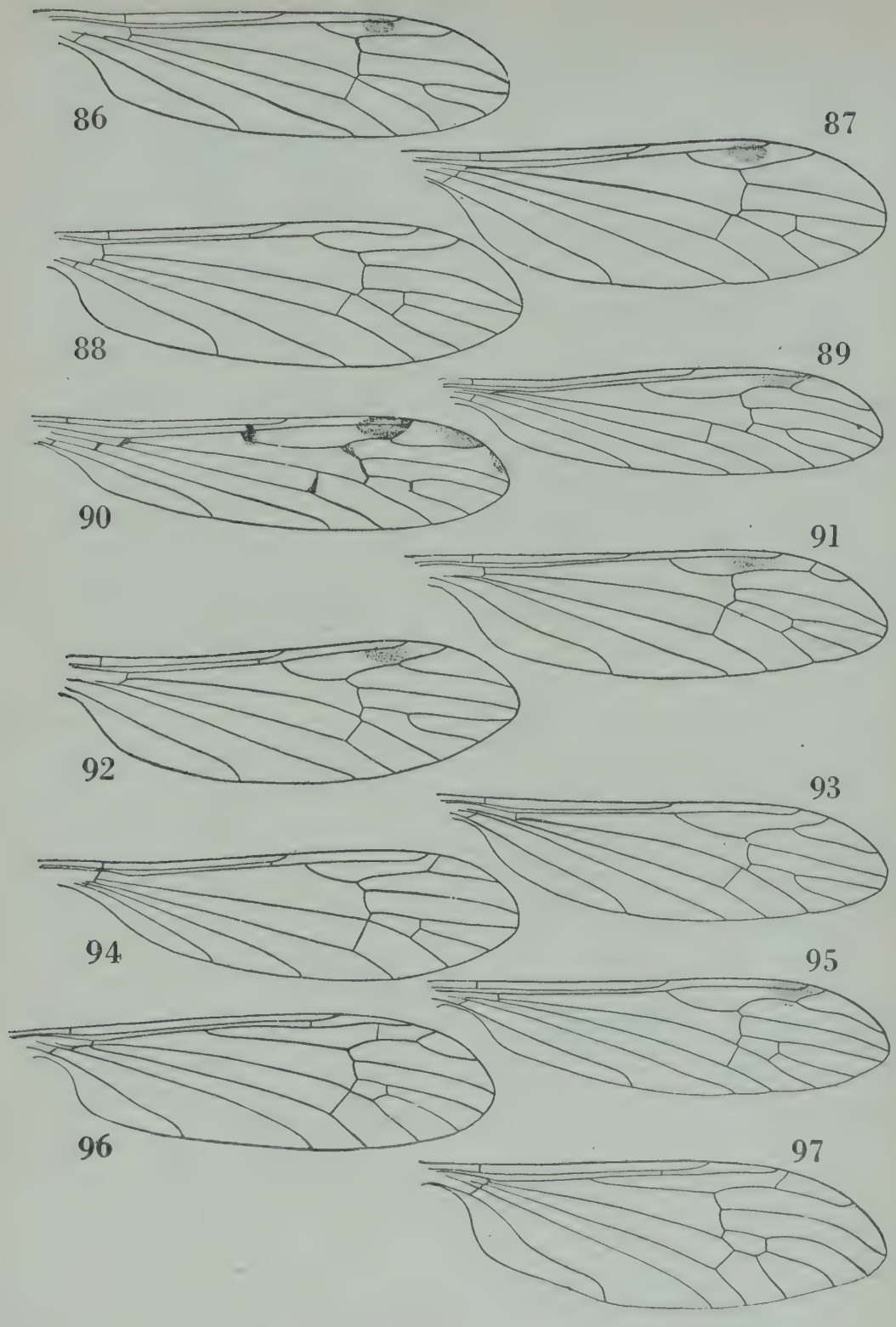

WINGS OF TIPULIDAE (ERIOPTERINI)

54, *Ormosia nubila*. 55, *O. apicalis*. 56, *O. innocens*. 57, *O. nigripila*. 58, *O. pygmaea*. 59, *O. nimbipennis*. 60, *O. rubella*. 61, *O. meigenii*. 62, *O. monticola*. 63, *O. mesocera*. 64, *O. megacera*
65, *Molophilus hirtipennis*. 66, *M. pubipennis*. 67, *M. fultonensis*. 68, *M. nova-caesariensis*. 69 *M. comatus*. 70, *M. ursinus*



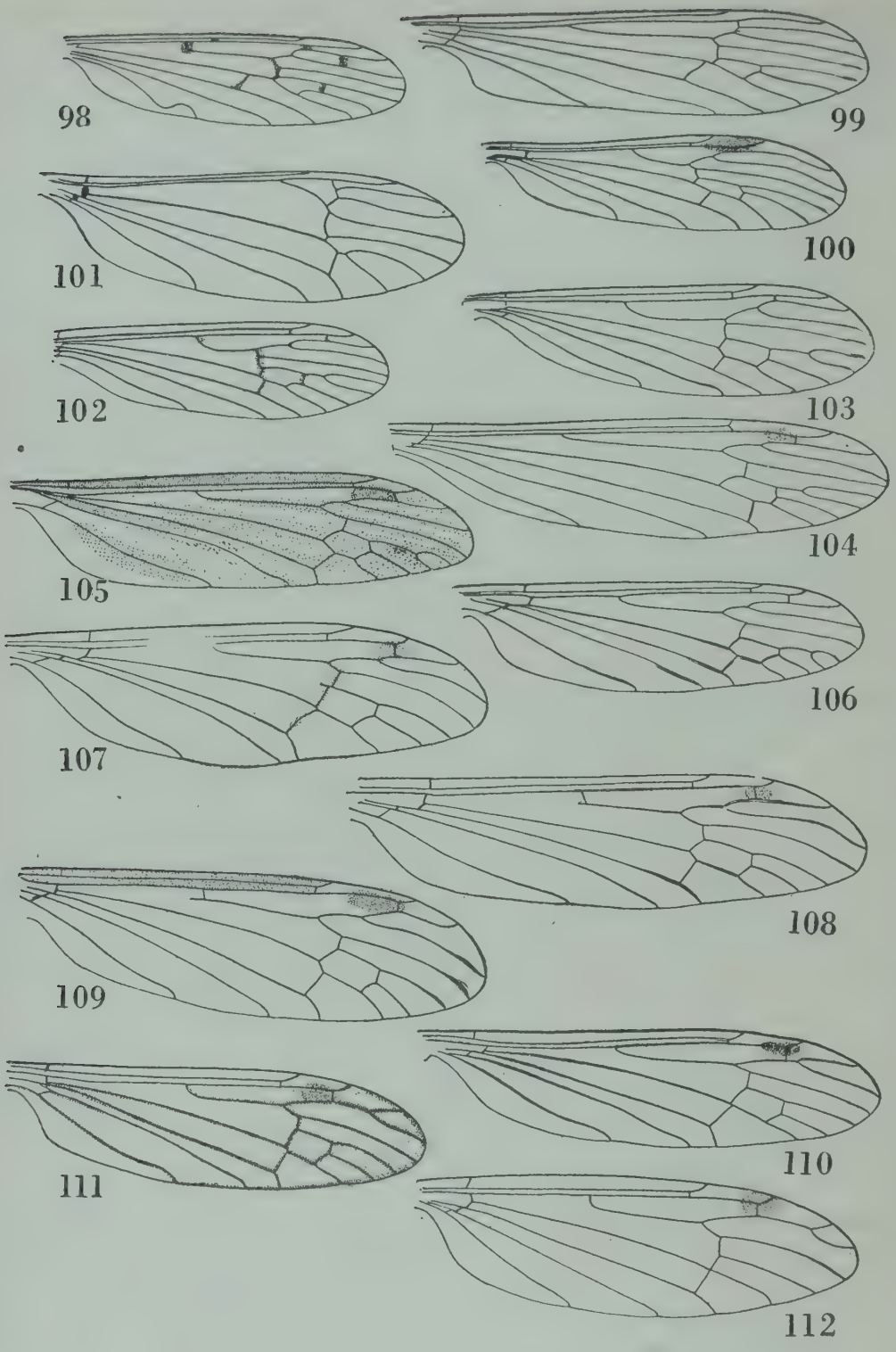

WINGS OF TIPULIDAE (ERIOPTERINI)

71, *Erioptera villosa*. 72, *E. septemtrionis*. 73, *E. vespertina*. 74, *E. chrysocoma*. 75, *E. chlorophylla*. 76, *E. straminea*. 77, *E. caloptera*. 78, *E. needhami*. 79, *E. parva*. 80, *E. venusta*. 81, *E. armillaris*. 82, *E. graphica*. 83, *E. armata*. 84, *E. nyctops*. 85, *E. stigmatica*



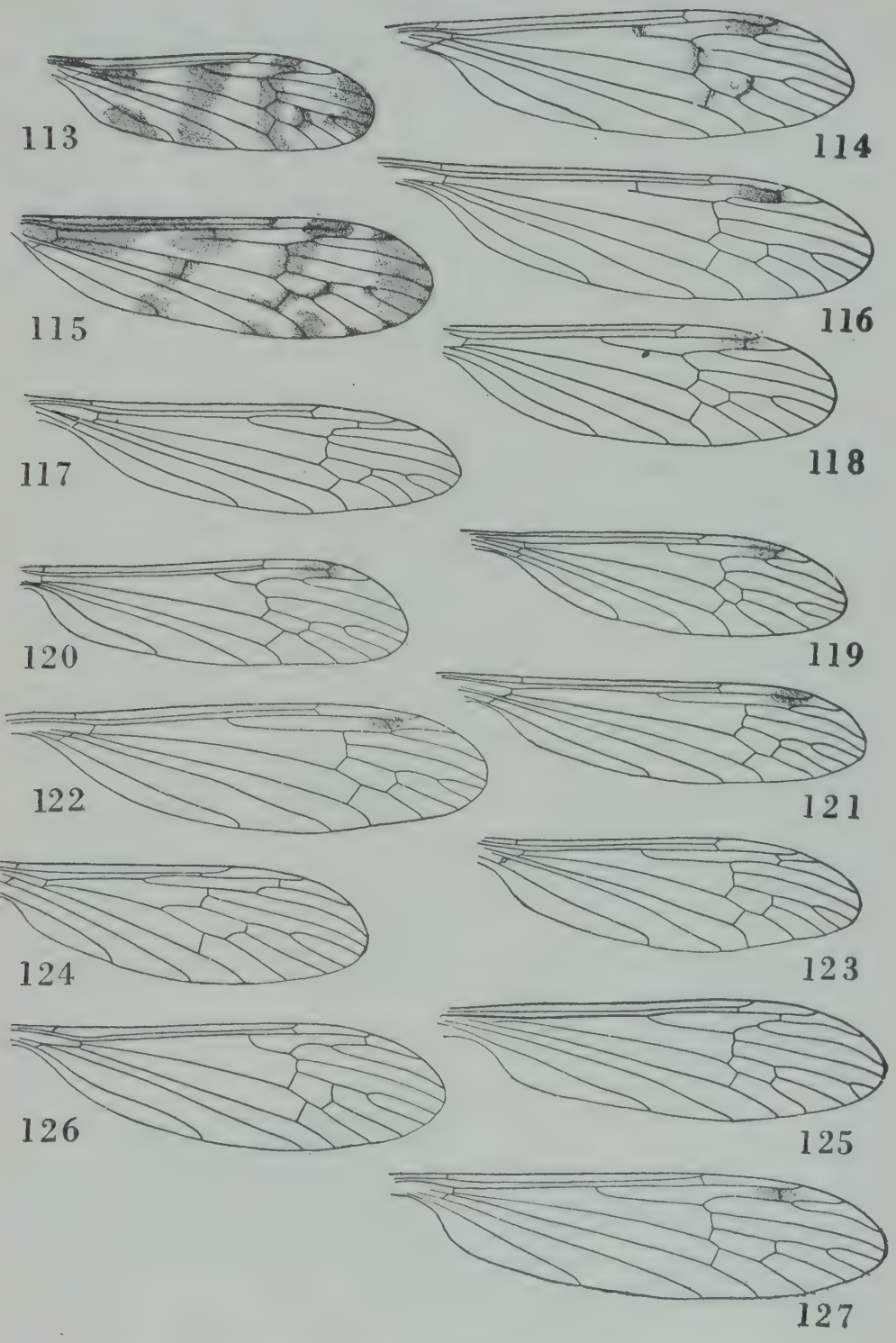

WINGS OF TIPULUDAE (ERIOPTERINI)

86, *Gonomyia alexanderi*. 87, *G. sacandaga*. 88, *G. manca*. 89, *G. mathesoni*. 90, *G. blanda*. 91, *G. sulphurella*. 92, *G. florens*. 93, *G. cognatella*. 94, *G. noveboracensis*. 95, *G. subcinerea*
96, *Rhabdomastix caudata*. 97, *R. flava*



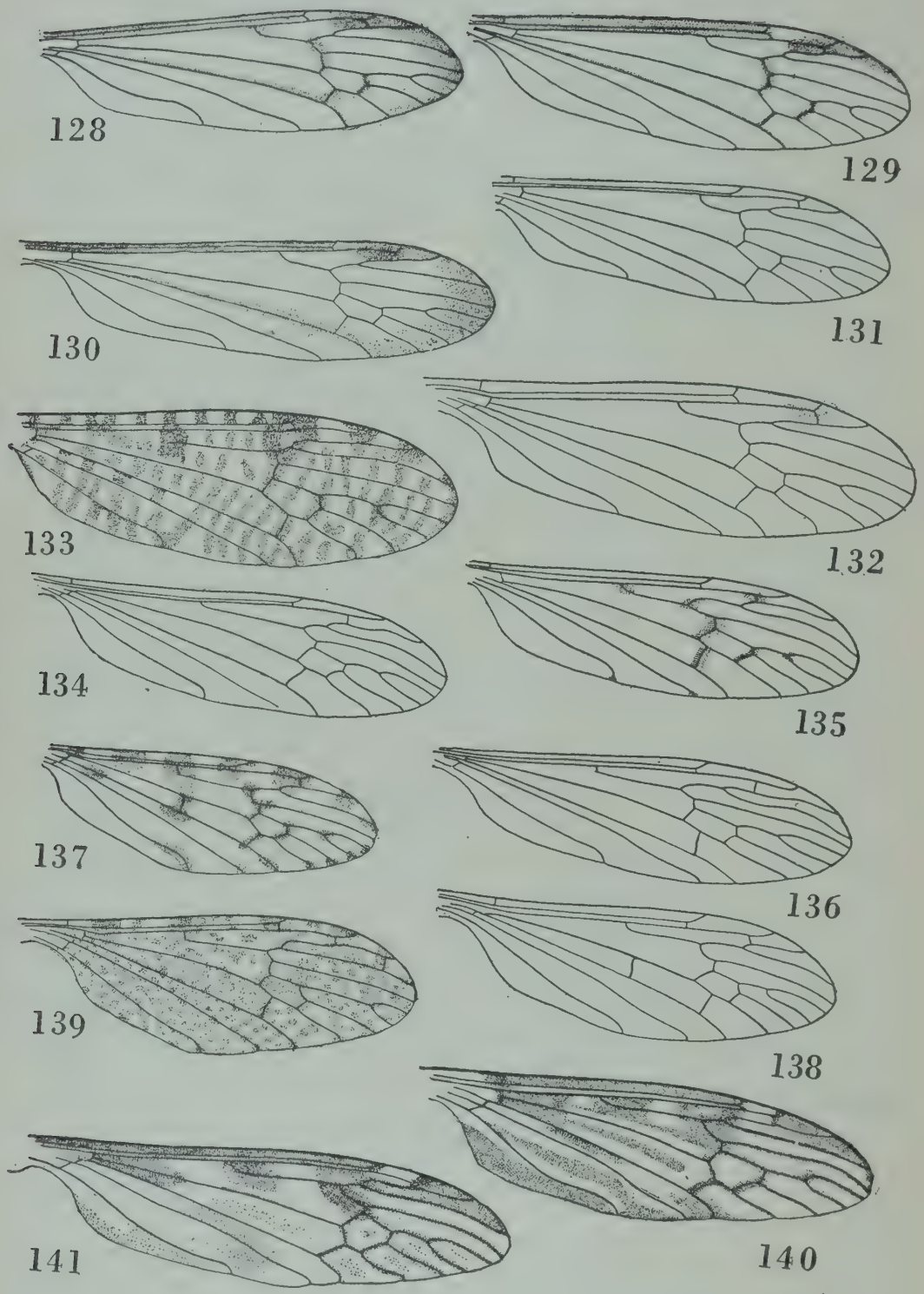

WINGS OF TIPULIDAE (ERIOPTERINI, HEXATOMINI)

98, *Helobia hybrida.* 99, *Trimicra anomala.* 100, *Gnophomyia tristissima.* 101, *Cryptolabis paradoxa.* 102, *Cladura flavoferruginea*; 103, *C. delicatula* 104, *Penthoptera albitarsis.* 105, *Eriocera spinosa*; 106, *E. brachycera*; 107, *E. longicornis*; 108, *E. cinerea*; 109, *E. wilsonii*; 110, *E. tristis*; 111, *E. fultonensis.* 112, *Hexatoma megacera*



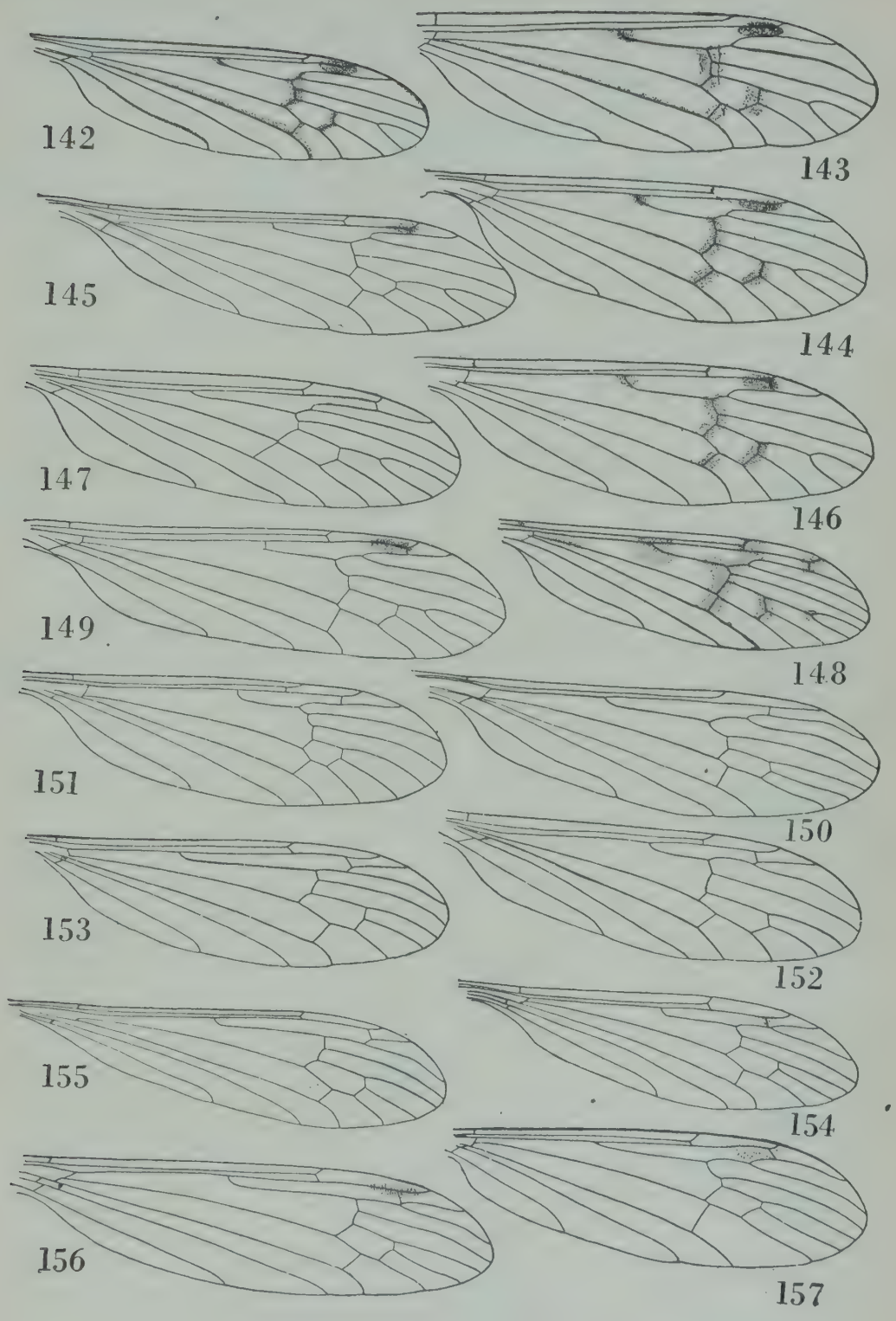

WINGS OF TIPULIDAE (LIMNOPHILINI)

113, *Limnophila macrocera*. 114, *L. unica*. 115, *L. fasciolata*. 116, *L. poetica*. 117, *L. tenuicornis*. 118, *L. niveitarsis*. 119, *L. albipes*. 120, *L. laricicola*. 121, *L. tenuipes*. 122, *L. imbecilla*. 123, *L. recondita*. 124, *L. areolata*. 125, *L. brevifurca*. 126, *L. toxoneura*. 127, *L. ultima*



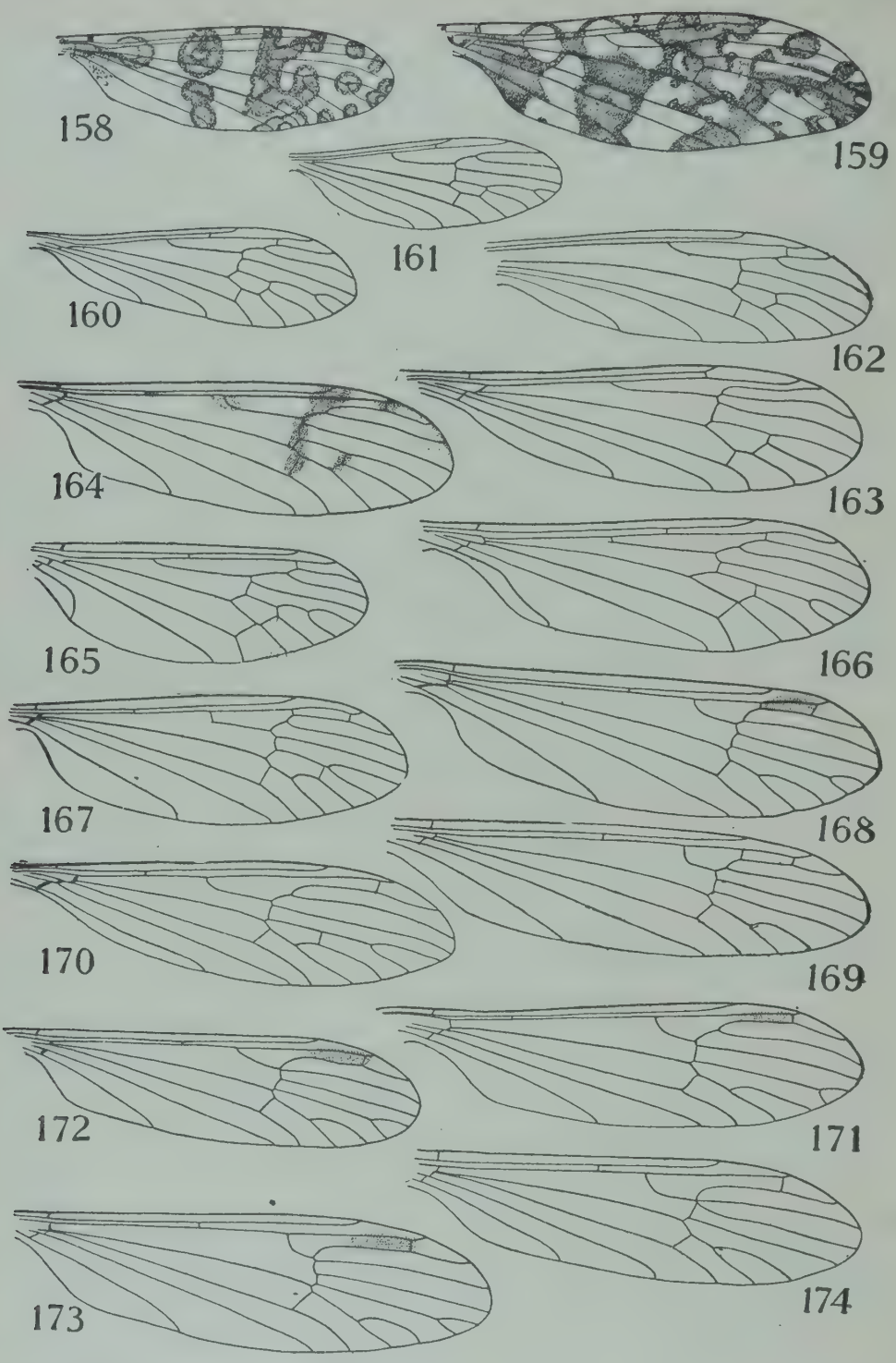

WINGS OF TIPULIDAE (LIMNOPHILINI)

128, *Limnophila adusta*. 129, *L. similis*. 130, *L. terrae-novae*. 131, *L. novae-angliae*. 132, *L. lutea*. 133, *L. irrorata*. 134, *L. inornata*. 135, *L. luteipennis*. 136, *L. nigripleura*. 137, *L. aprilina*. 138, *L. johnsoni*. 139, *L. fuscovaria*. 140, *L. alleni*. 141, *L. marchandi*



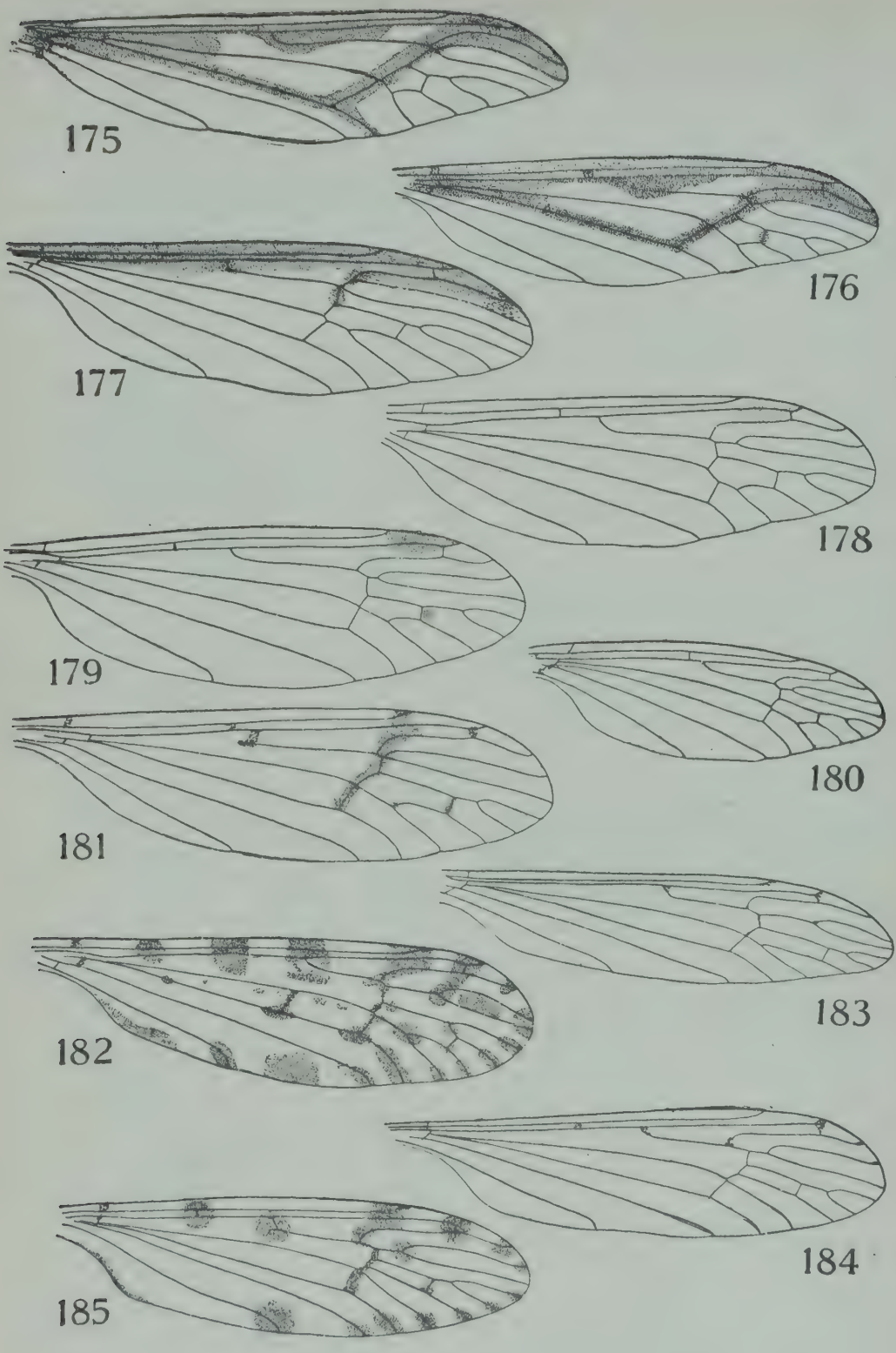

WINGS OF TIPULIDAE (LIMNOPHILINI)

142, *Limnophila rufibasis*. 143, *L. simplex*. 144, *L. munda*. 145, *L. mundoides*. 146, *L. terebrans*. 147, *L. cubitalis*. 148, *L. montana*. 149, *L. subcostata*. 150, *L. noveboracensis*. 151, *L. emmelina*. 152, *L. lenta*. 153, *L. quadrata*. 154, *L. osborni*. 155, *L. stanwoodae*. 156, *L. edwardi*. 157, *L. sylvia*



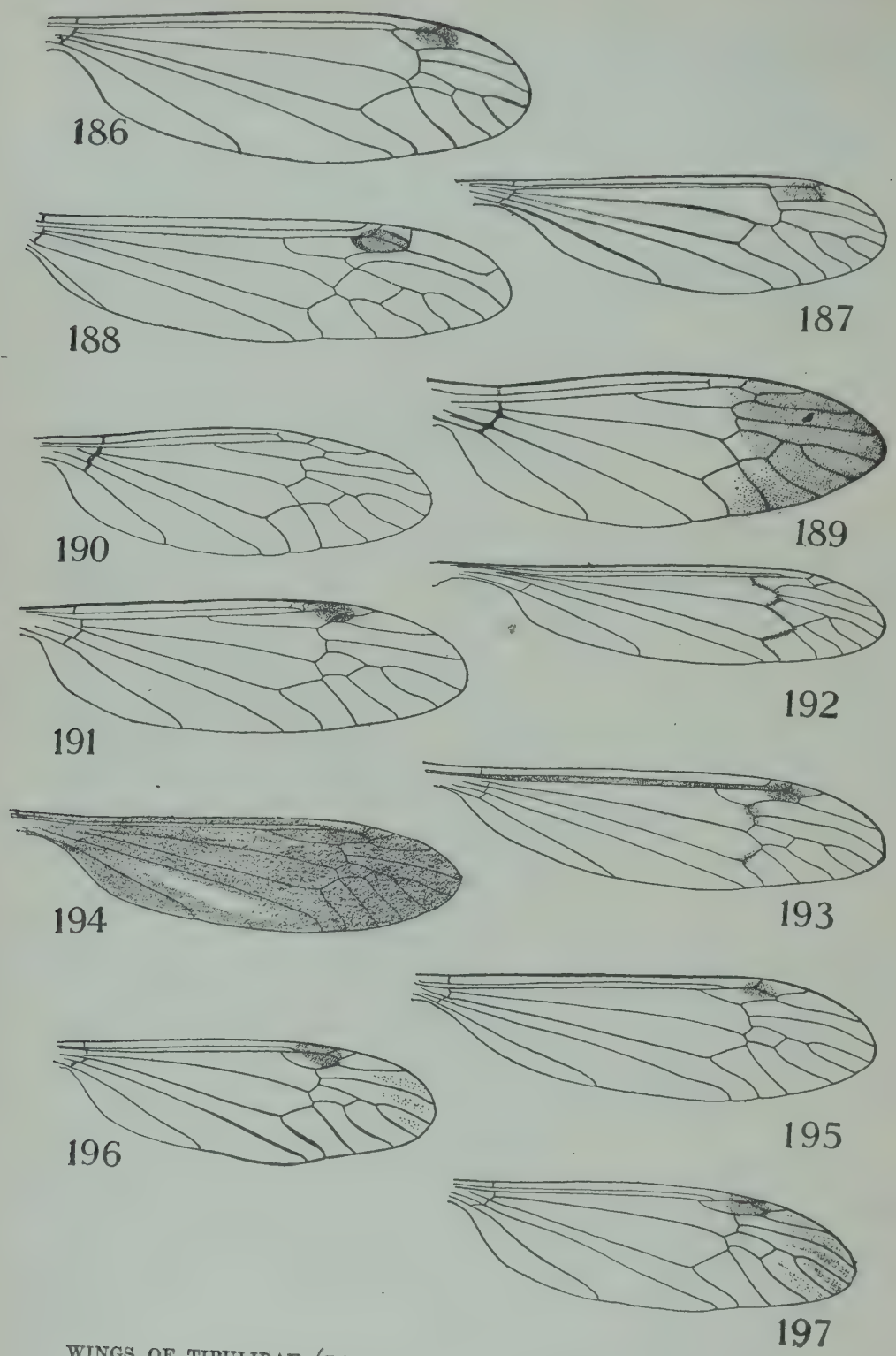

WINGS OF TIPULIDAE (LIMNOPHILINI, PEDICIINI), AND TWO SPECIES IN RHYPHIDAE

158, *Epiphragma fascipennis*; 159, *E. solatrix*. 160, *Adelphomyia americana*; 161, *A. minuta*; 162, *A. cayuga*. 163, *Ulomorpha pilosella*. 164, *Ula elegans* 165, *Trichocera brumalis*; 166, *T. subsinuata* 167, *Dicranota pallida*; 168, *D. noveboracensis*; 169, *D. rivularis*. 170, *Rhaphidolabis flaveola*; 171, *R. tenuipes*; 172, *R. rubescens*; 173, *R. cayuga*; 174, *R. modesta*




WINGS OF TIPULIDAE (PEDICIINI)

175, *Pedicia albivitta*. 176, *P. contermina* 177, *Tricyphona inconstans*. 178, *T. calcar*. 179, *T. autumnalis*, male; 180, *T. autumnalis*, female. 181, *T. auripennis*. 182, *T. hyperborea*. 183, *T. katahdin*. 184, *T. paludicola*. 185, *T. vernalis*

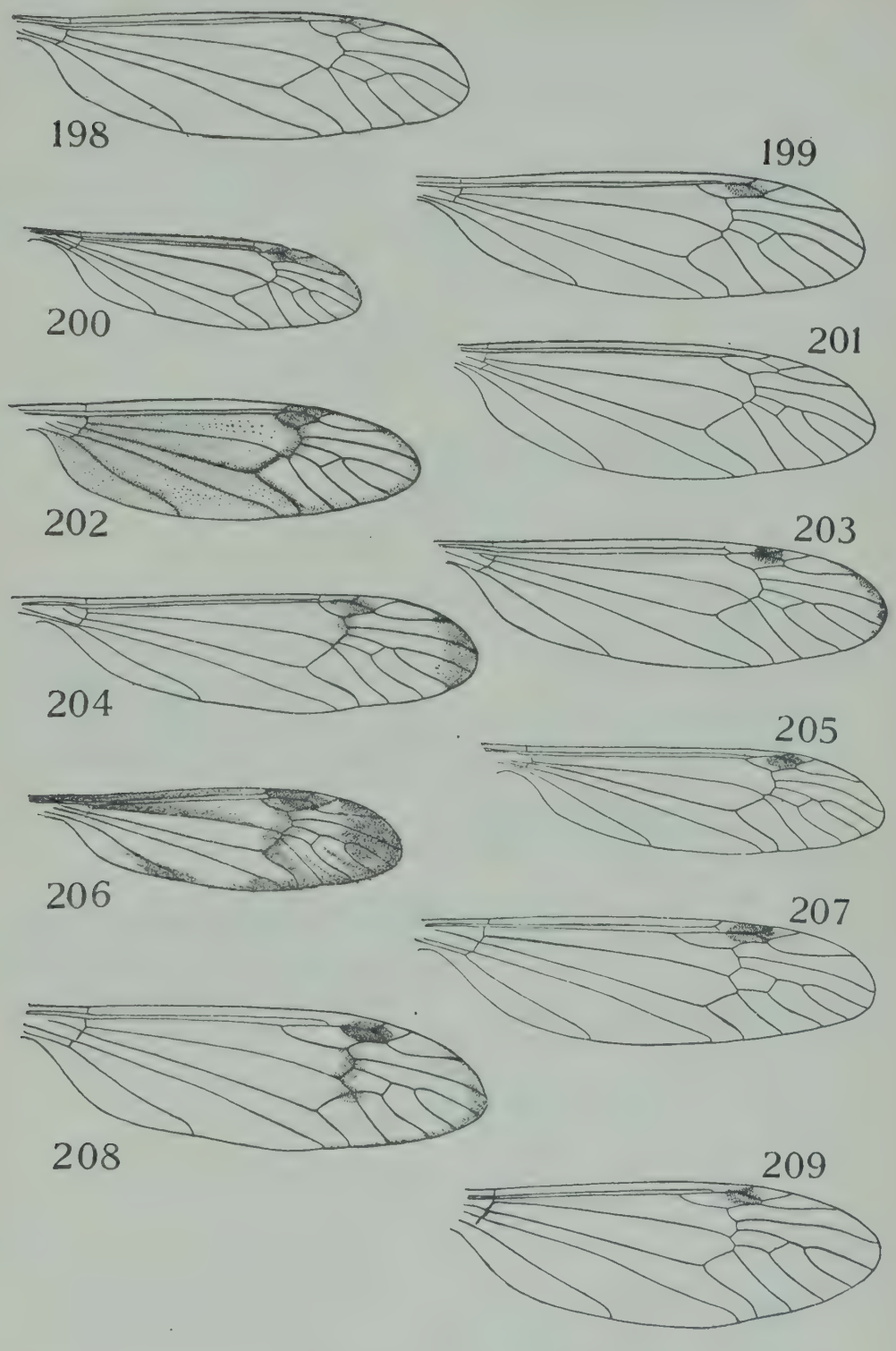



WINGS OF TIPULIDAE (DOLICHOPEZINI, CTENOPHORINI, TIPULINI)

186, *Oropeza obscura.* 187, *Dolichopeza americana.* 188, *Brachypremna dispellens*

189, *Ctenophora apicata*, normal form; 190, *C. apicata*, black form. 191, *Tanyptera frontalis*

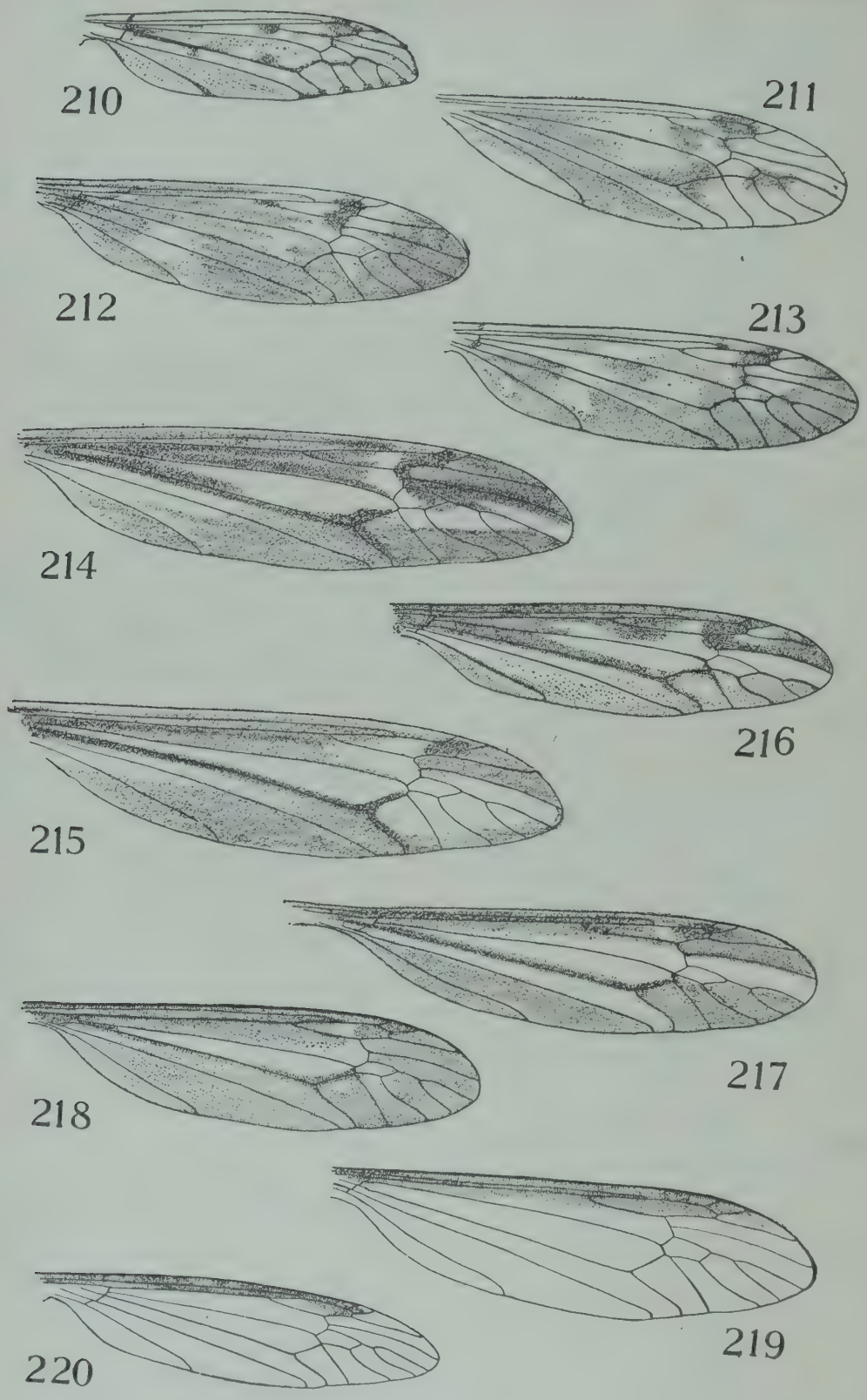
192, *Longurio testaceus*; 193, *L. minimus.* 194, *Stygeropis fuscipennis.* 195, *Tipula oropezoides*; 196, *T. unimaculata*; 197, *T. algonquin*




WINGS OF TIPULIDAE (TIPULINI)

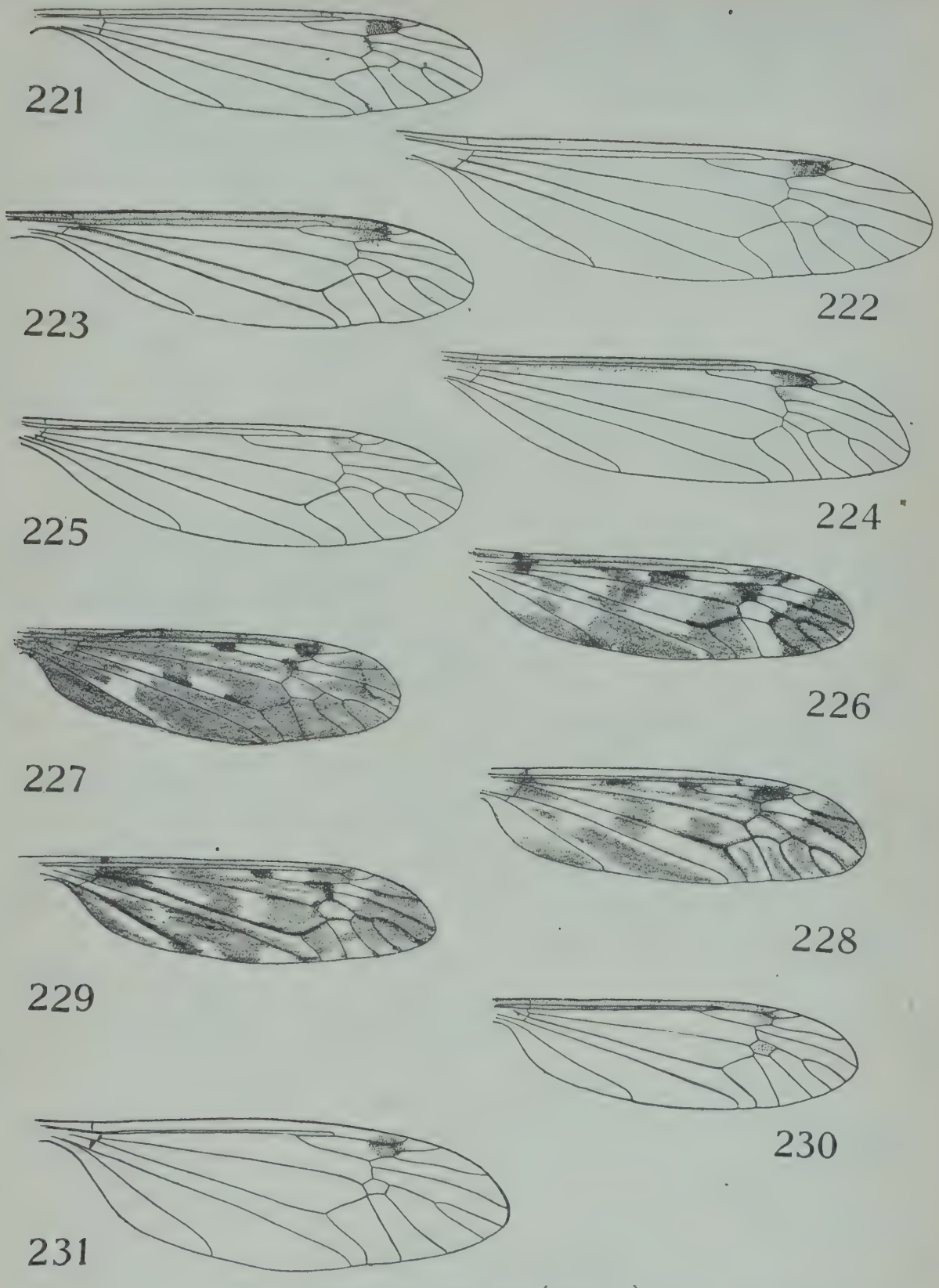
198, *Nephrotoma ferruginea.* 199, *N. tenuis.* 200, *N. macrocera.* 201, *N. xanthostigma.* 202, *N. lugens.* 203, *N. pedunculata.* 204, *N. incurva.* 205, *N. penumbra*

206, *Tipula unifasciata.* 207, *T. collaris.* 208, *T. nobilis.* 209, *T. pachyrhinoides*



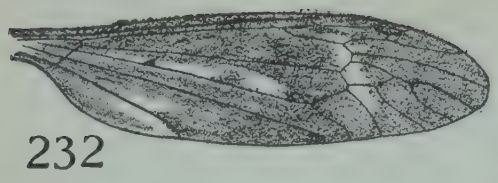

WINGS OF TIPULIDAE (TIPULINI)

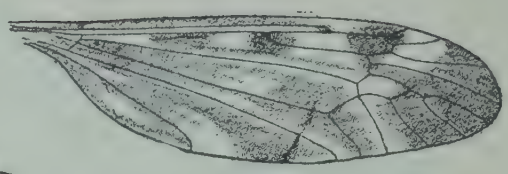
210, *Tipula abdominalis*. 211, *T. hermannia*. 212, *T. angustipennis*. 213, *T. senega*. 214, *T. caloptera*. 215, *T. strepens*. 216, *T. bella*. 217, *T. eluta*. 218, *T. tricolor*. 219, *T. sayi*. 220, *T. cunctans*

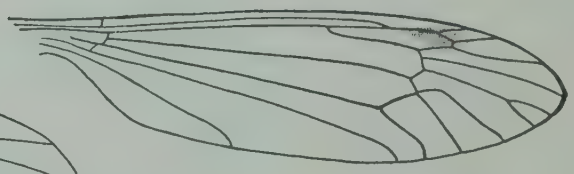


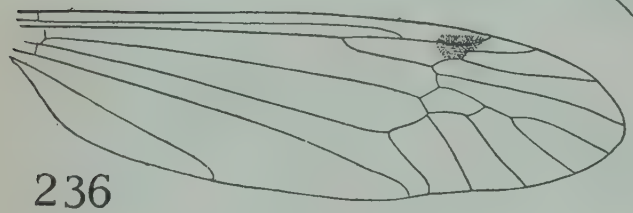

WINGS OF TIPULIDAE (TIPULINI)

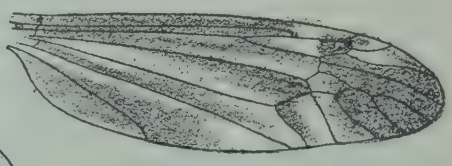
221, *Tipula tephrocephala*. 222, *T. cayuga*. 223, *T. perlongipes*. 224, *T. kennicotti*. 225, *T. sulphurea*. 226, *T. trivittata*. 227, *T. balioptera*. 228, *T. labradorica*. 229, *T. longiventris*. 230, *T. bicornis*. 231, *T. megaura*

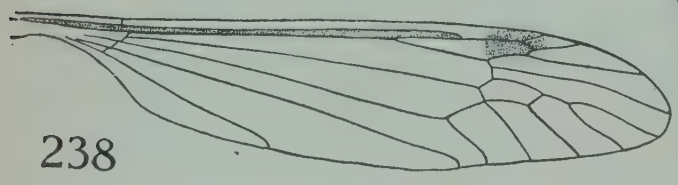


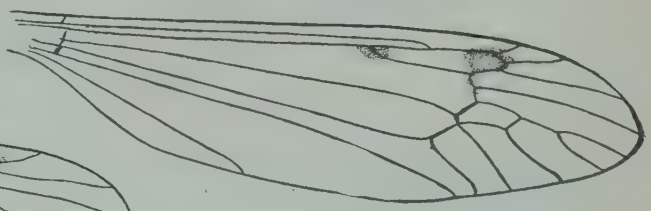



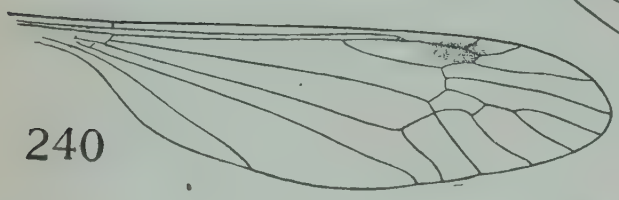


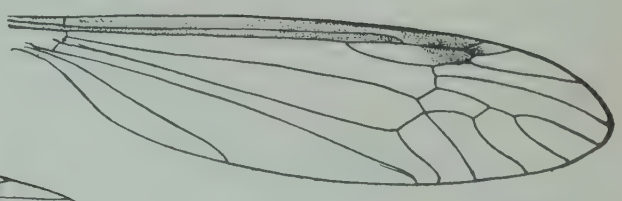



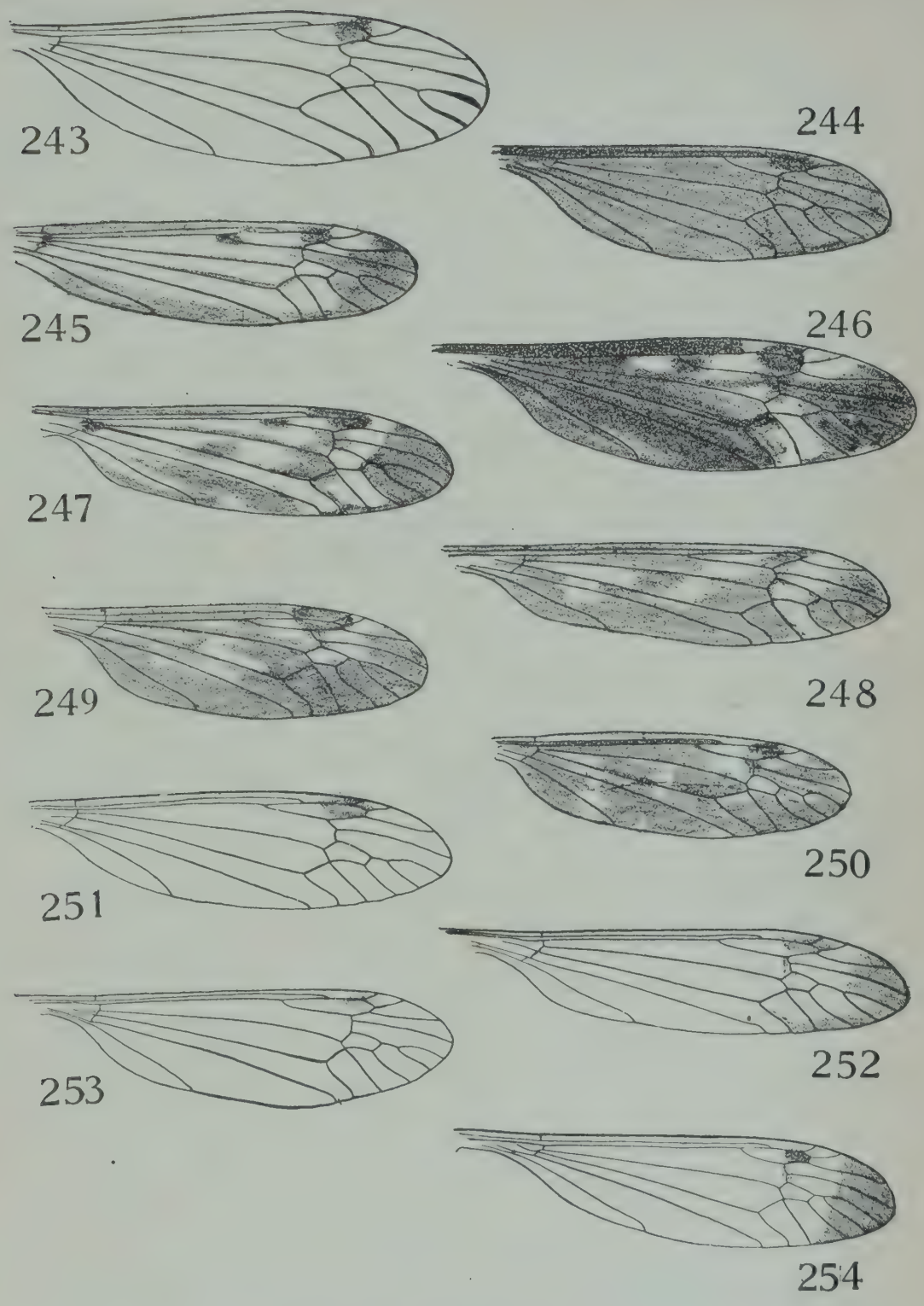



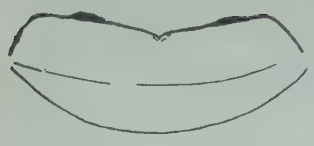
WINGS OF TIPULIDAE (TIPULINI)

232, *Tipula ultima*. 233, *T. macrolabis*. 234, *T. locwiana*. 235, *T. aperta*. 236, *T. umbrosa*. 237, *T. valida*. 238, *T. dietziana*. 239, *T. submaculata*. 240, *T. triton*. 241, *T. tuscarora*. 242, *T. mingwe*




WINGS OF TIPULIDAE (TIPULINI)

243, *Tipula annulicornis*, male. 244, *T. taughannock*, female. 245 and 246, *T. fuliginosa*, male and female. 247, *T. penobscot*. 248, *T. subfasciata*. 249, *T. hebes*. 250, *T. fragilis*. 251, *T. dejecta*. 252, *T. iroquois*. 253, *T. mainensis*. 254, *T. apicalis*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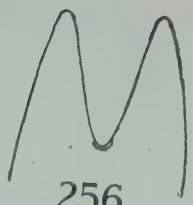
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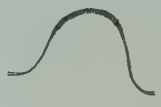
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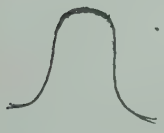
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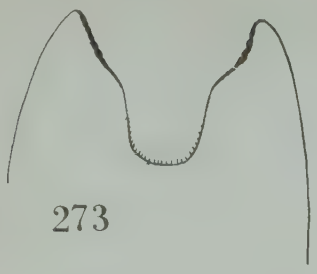

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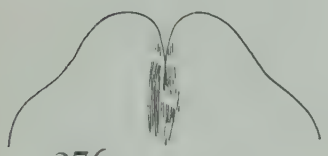

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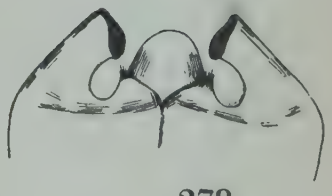

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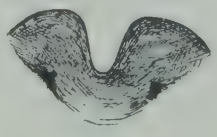

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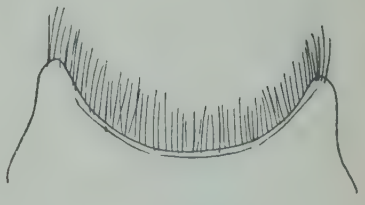

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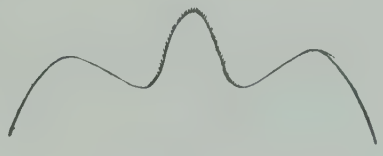

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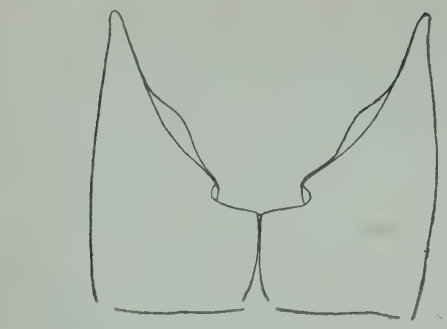
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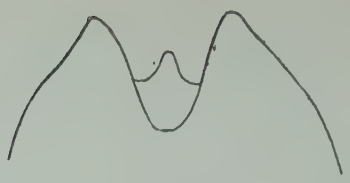
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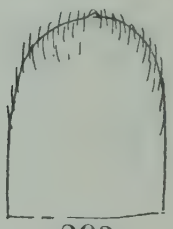
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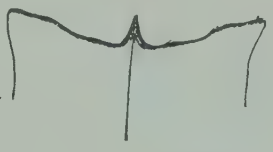
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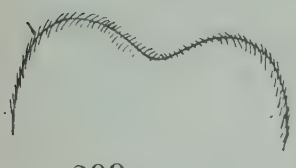
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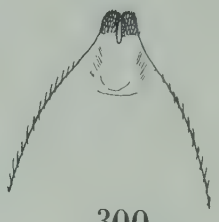
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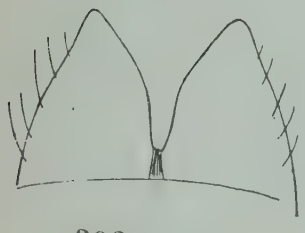
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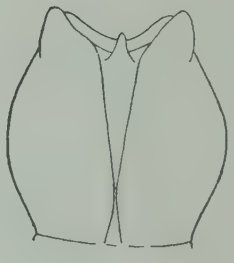
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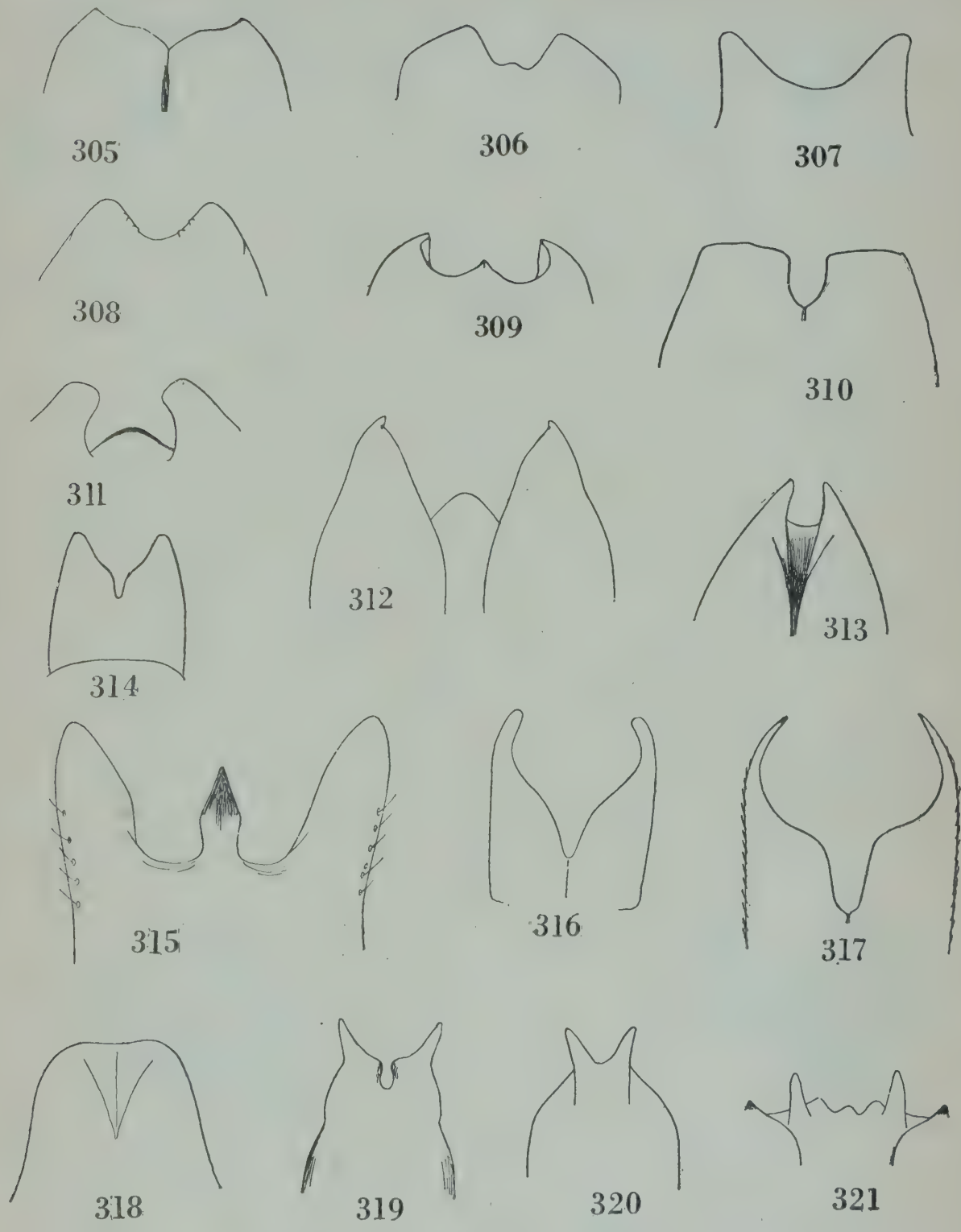


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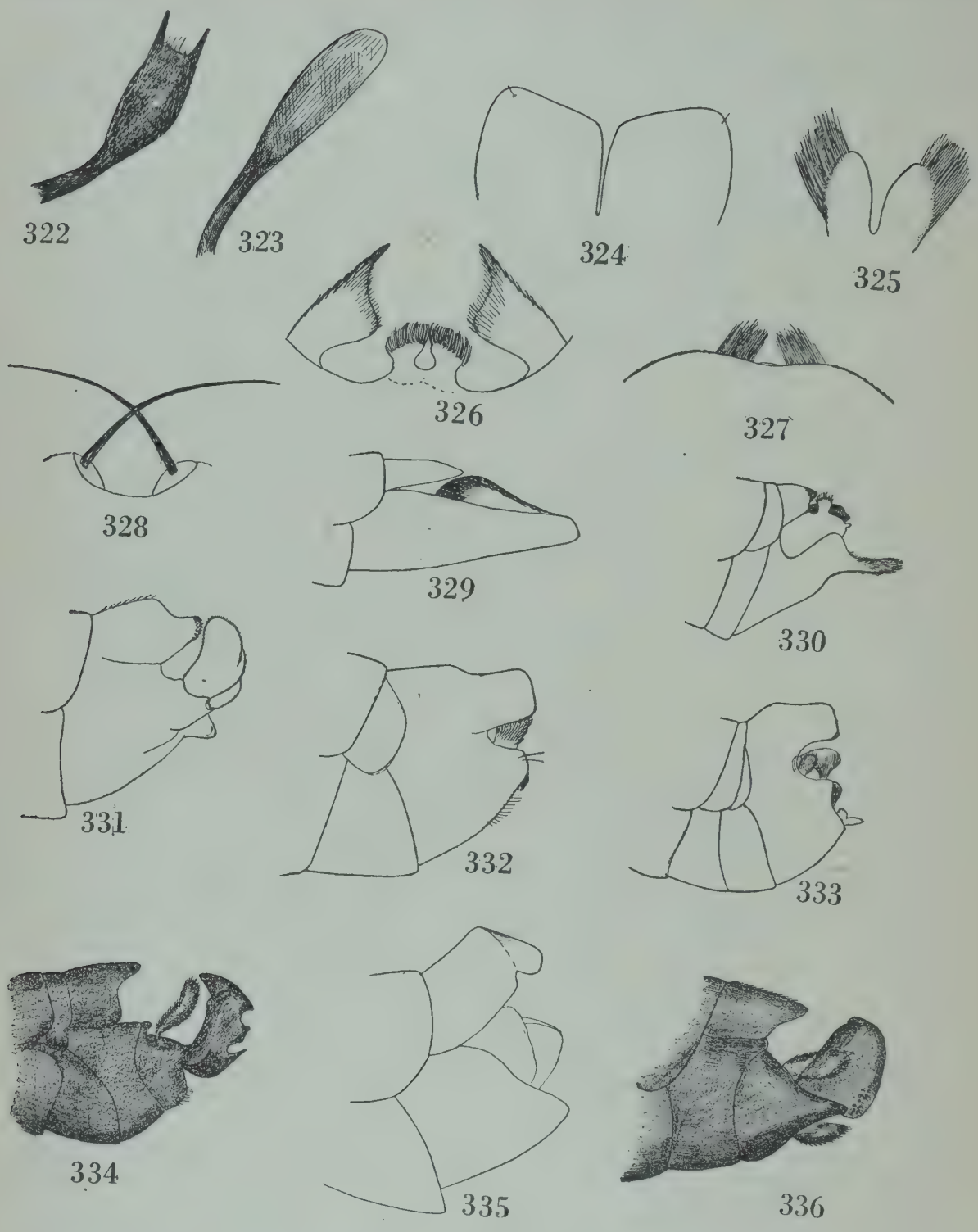


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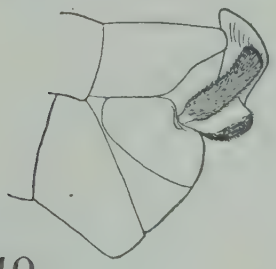

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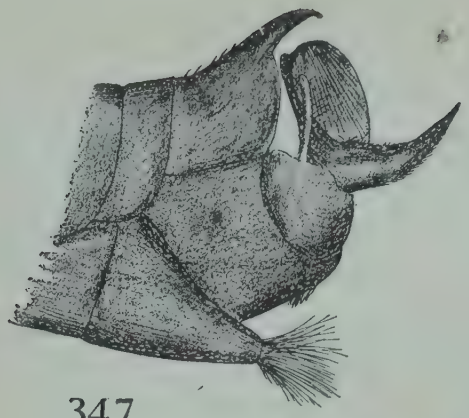

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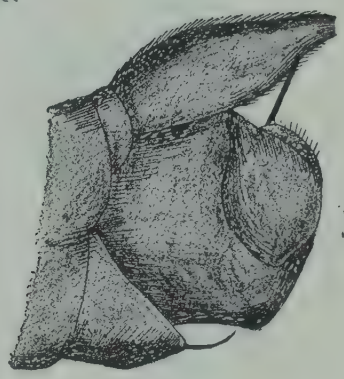

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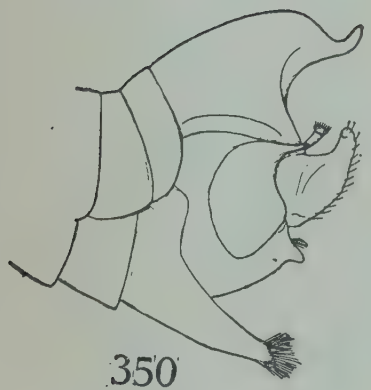

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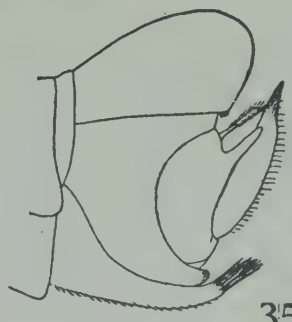

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AGRICULTURAL EXPERIMENT STATION

# THE DRY ROOT-ROT OF THE BEAN

WALTER H. BURKHOLDER

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# THE DRY ROOT-ROT OF THE BEAN

# THE DRY ROOT-ROT OF THE BEAN

WALTER H. BURKHOLDER [1]

Very little consideration has been given to the diseases that affect the bean plant (*Phaseolus vulgaris* L.) below ground. During the past few seasons an investigation of bean diseases in New York State by the writer has shown that such diseases are very common and frequently very destructive. The most important of these, and one that is enphytotic to the western bean section of the State, is the dry root-rot. This disease affects all the commercial varieties of the dry shell beans, and, so far as known, all those used for canning purposes. The dry root-rot may occur also on other species of Phaseolus. The following are affected: the tepary bean (*P. acutifolius* Gray var. *latifolius* Freeman), the scarlet runner bean (*P. multiflorus* Willd.), the moth bean (*P. aconitifolius* Jacq.), the lima bean (*P. lunatus* L.), and the adzuki bean (*P. angularis* Willd.). The disease has likewise been observed on the Black-eye cowpea (*Vigna sinensis* [L.] Endl.) and the kulti bean (*Dolichos biflorus* L.).

In New York State the disease is of general occurrence. It has been observed in 90 per cent of the bean fields of the six largest bean-producing counties, and is found wherever the crop has been grown to any extent. Specimens of bean plants affected with the dry root-rot have been received from A. H. Gilbert and G. A. Meckstroth, of the United States Bureau of Plant Industry, collected at Burlington, Vermont, and Grand Rapids, Michigan, respectively.

It is not known when the dry root-rot first appeared in New York State. A few growers claim to have observed it for at least twenty-five years. Since it is now of such general distribution in the bean sections, apparently it must have been present for a long time. As far as known, no reference to this disease has ever been made in literature except by the writer (1916 and 1917), and these references apply to New York State. The disease therefore evidently originated in this region or was introduced from a locality where it has not attracted attention. The symptoms of the disease above ground are not striking and could readily be mistaken

[1] The writer wishes to acknowledge his indebtedness to Dr. Donald Reddick for helpful suggestions and criticisms during the progress of this work.

for the result of unfavorable weather conditions. Thus, where the disease is not abundant it could easily be overlooked.

In New York State where the dry root-rot is common, severe losses to the bean crop result. It is a matter of common observation that there has been during the past ten years a marked decrease in the bean yield. The decrease has been estimated by a number of the large growers and seedsmen to be approximately 25 per cent. The writer, from observations in the bean section, is led to the conclusion that no small part of this decrease is due to the dry root-rot.

## SYMPTOMS OF THE DISEASE

### ON THE ROOTS AND OTHER UNDERGROUND PARTS

The first signs of the disease on the bean show a week or two after the plant has appeared above ground. At this time there may be observed

FIG. 133. THE DRY ROOT-ROT OF THE BEAN

At left, root of a White Marrow bean affected with dry root-rot. At right, a healthy root; the strong lateral roots branching off from the lower end of the taproot are evident

on the taproot a reddish discoloration, but the morphology of the root remains normal. The discoloration may cover the taproot and have no

DRY ROOT-ROT OF BEAN

1, A field of White Marrow beans affected with dry root-rot. The rows are 28 inches apart. Healthy plants would cover the ground

2, The dry root-rot of the bean. A mass of surface roots has been produced above the dried taproot

3, Flat Marrow bean resistant to dry root-rot. The effect of the disease is shown on the White Marrows near the Flat Marrow

EFFECT OF DRY ROOT-ROT ON THE PARTS OF THE WHITE MARROW BEAN PLANT ABOVE GROUND

The diseased plant has failed to vine. Also the pods are few in number and are poorly filled

definite margin, or may occur as red streaks which frequently extend to or above the surface of the ground. Later the diseased areas become brown and longitudinal fissures appear in the cortex.

As the disease progresses upward, the lower lateral roots and the end of the taproot shrivel and become dry. Frequently, too, the main root and the lower part of the stalk are found to be pithy. Above the dead area new lateral roots are developed. These frequently push their way through the diseased cortex and subsequently become diseased. Other roots that are produced above the lesions may develop rapidly and become abnormally large, to take the place of the diseased lower rootlets. Occasionally one of these lateral roots takes the place of the taproot. More frequently, however, these surface roots are small and very numerous, and form a dense mat in the first inch or so of soil (Plate LVI, 2). As a rule they do not become severely affected, and persist throughout the entire growing season. On the other hand, in severe cases the entire root system may be destroyed.

### ON THE PLANT ABOVE GROUND

Although no lesions appear above ground, the effect of the loss of the lower lateral roots and part of the taproot is very noticeable. This is especially true during the latter part of the growing season. During the first five to six weeks of growth a diseased plant may not be readily detected unless in comparison with a healthy one. At this stage the affected plant is slightly dwarfed but otherwise remains normal in appearance so far as the parts above ground are concerned. The symptoms of the disease are more evident at podding time. There is then an apparent checking in growth of the entire plant. Few pods are formed, and the remainder either fail to set, or drop in the early stages of their formation (Plate LVII). The leaves of plants affected with the dry root-rot frequently turn yellow and fall. This has given rise in some localities to the name *yellow-leaf*, but it is a character which is not constant. Nevertheless, the diseased individuals mature earlier than do normal plants, since they dry much more rapidly in the absence of an entire root system. The seeds also in the few pods frequently are under size, and this contributes to the loss in yield.

In the true sense of the word this disease is not a wilt, as the leaves or the tender parts of the plant seldom flag. In a few cases, however,

the writer has observed a distinct wilting of the plants. In these latter cases all the leaves dropped and turned brown, and persisted on the plant. The small pods withered and clung to the stem, while the older pods matured a few small seeds. A condition similar to this has frequently been observed which is due to the bacterial blight caused by *Bacterium phaseoli* E. F. Smith. Careful examination, however, may distinguish between the two diseases.

The general appearance of fields of beans affected with the dry root-rot may vary. Whenever the disease occurs in a field, approximately 100 per cent of the plants show the symptoms. All the plants may appear uniform (Plate LVI, 1); on the other hand, certain parts of the field frequently are affected more severely than others, thus giving the appearance that the disease occurs in limited areas. There are several possible explanations for this spotted condition. One is that the soil conditions are not uniform; a second is that frequently wireworms or other insects attack the decaying roots and complete their destruction.

## SYMPTOMS OF OTHER ROOT DISEASES OF THE BEAN

Two other root diseases of the bean in New York State might be confused with the dry root-rot. They are the black root-rot, caused by *Thielavia basicola* Zopf., and a blotch caused by Rhizoctonia. In the greenhouse, species of Botrytis, Fusarium, and various other fungi attack the young seedling at the surface of the ground or cause more or less of a root disturbance. These fungi have seldom been observed in the field.

### *Black root-rot*

The black root-rot in New York State is local in its distribution. It has been observed only along the southern edge of the dry-shell-bean district. In its early stages this disease is scarcely distinguishable from the dry root-rot. The discoloration of the taproot at times may appear to be somewhat purple in contrast to the orange-red color produced by the dry root-rot. Otherwise the two diseases are very similar. Later in the season, coal-black lesions, which are very characteristic, appear on the affected roots. These lesions may vary from small streaks to cankers which encircle half the taproot and completely envelop many of the lateral roots. Frequently during damp weather a frosty appearance may

be noticed over the lesions and the diseased parts of the plants. This is due to the large production of the so-called endoconidiophores belonging to *Thielavia basicola*. Since this disease is often observed associated with the dry root-rot, the two groups of symptoms may be found together.

It has been the observation of the writer that the black root-rot occurs more generally during the early part of the growing season, and at times affects germination. Frequently plants affected with this disease may be able to throw it off by the middle of August, and late infection causes no serious injury to the root system. These two observations have been further substantiated by the writer through inoculation experiments. The symptom of the dry root-rot, on the other hand, is more evident during the latter part of the season.

### *Rhizoctonia blotch*

The Rhizoctonia blotch in New York State is of general distribution but has never been observed to cause any appreciable losses. Brick-red blotches are produced mainly on the taproot and on the bean stem near the surface of the ground. The lateral roots are seldom affected. The lesions caused by Rhizoctonia are sunken, and usually irregular but definite in outline. This is the most distinguishing characteristic of the disease, and as a rule readily separates it from the other root diseases of the bean.

## ETIOLOGY

The dry root-rot disease of the bean is caused by the fungous pathogene *Fusarium martii phaseoli* n. form.

## MORPHOLOGY

The pathogene causing dry root-rot of the bean has the following morphological characters:

Macroconidia mostly 3-septate (44.5 x 5.1 $\mu$), 4-septate (50.09 x 5.3 $\mu$), rarely 5-septate, of nearly even diameter throughout, more or less curved near apex, with somewhat rounded or but slightly pointed apex, usually apedicellate. Microconidia rare. Aerial mycelium in culture scanty and usually white. Spores borne mostly in pseudopionnotes. Cultures when mature from a lichen[2] and montpellier green (on synthetic agar [3])

[2] The colors are after Robert Ridgway's *Color Standards and Color Nomenclature.*
[3] Richard's solution with two per cent agar.

to a pale olive-buff or cinnabar-green (on potato agar), to a zinc-green and dusky green-blue (on potato plug), to a purple-drab (on steamed rice). Spores in mass frequently yellowish. Chlamydospores terminal or intercalary, single or in short chains (11.6 $\mu$ in diameter).

## CULTURAL CHARACTERS

In growing the fungus on various media, a marked variation in its microscopical appearance is seldom found. The intensity of color production, however, varies considerably, not only on different media but on the same medium with the presence or the absence of air. The colors, when produced, are of various shades of blue and green. The spore mass frequently has a yellowish appearance. The growth of *Fusarium martii phaseoli* on steamed rice differs greatly from that on any other medium used. The fungus on rice is purple-drab but the medium itself is colored a coral pink. Microscopically also there is a great change. The spores are very abnormal and a great number of microconidia are produced. On cellulose agar the fungous growth is very scanty and there is scarcely any digestion of the cellulose.

The proportion of conidium types (those bearing the same septations) and the conidium measurements do not vary greatly on the different agars and on sterilized vegetables. For making the measurements, the fungus was grown on six different media. In the majority of cases the media were the same as those used by Sherbakoff (1915 b) in his study of *Fusarium martii* Ap. and Wr. The age of the cultures also was similar; in most cases they were in a state of maturity. One hundred conidia taken at random were measured in each case. Types that occurred in a culture but were not found when measuring the spores were marked "rare." It was considered that such types were present in less than one per cent.

The measurements of the conidia were as follows:

On bean plugs, cultures eighty-three days old; conidia taken from pseudopionnotes:

Conidia: 3–septate, 38 per cent, 41.4 x 4.9 (37.7–46.5 x 3.9–5.8) $\mu$
4–septate, 62 per cent, 47 x 5 (40.3–53.3 x 4.5–5.8) $\mu$
5–septate, rare

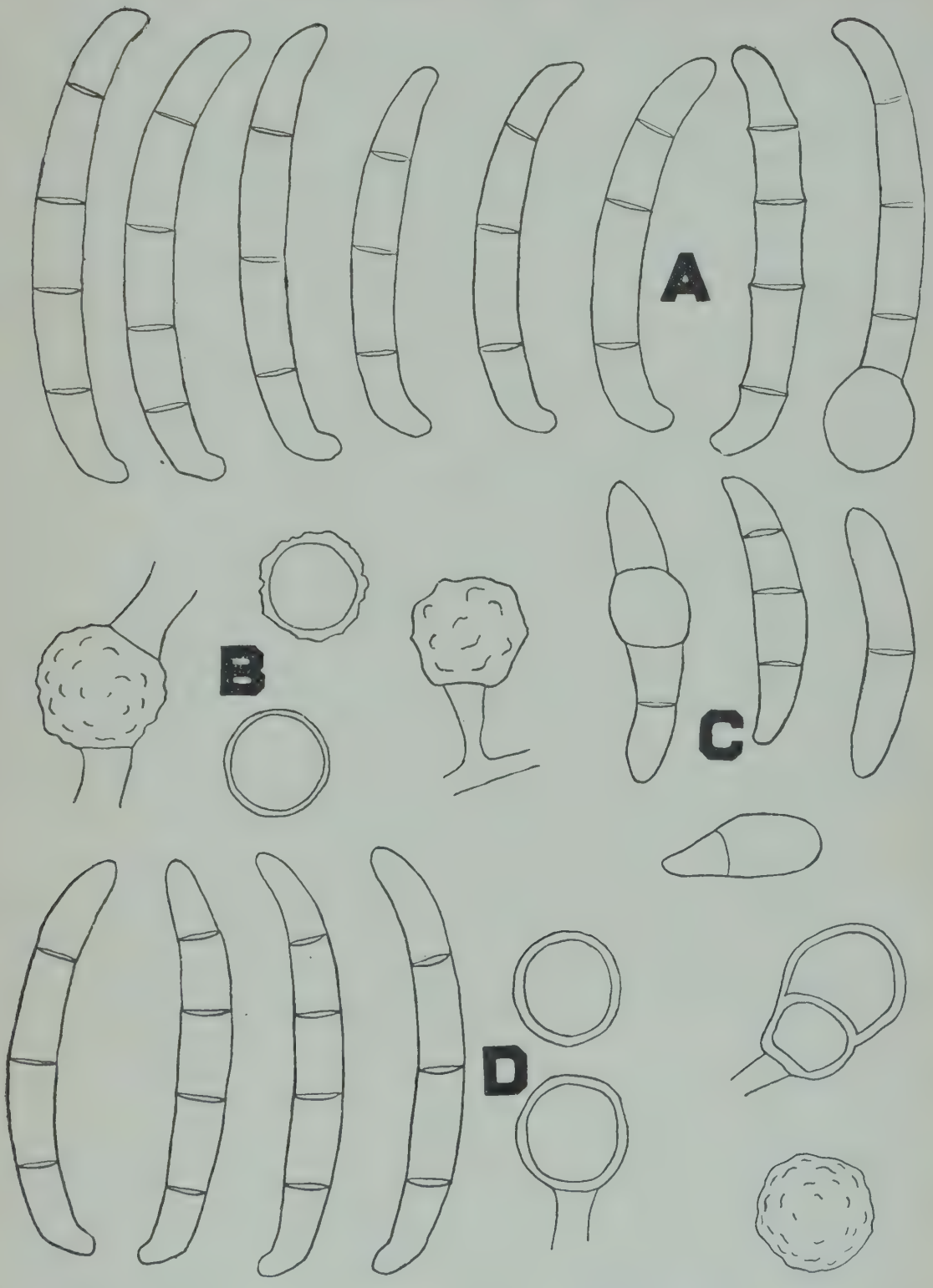


FIG. 134. SPORES OF FUSARIUM MARTII PHASEOLI

A, Macroconidia from sterilized bean plug cultures 83 days old; B, chlamydospores from the same culture; C, macroconidia from steamed rice, cultures 80 days old; D, macroconidia and chlamydospores from potato agar cultures 70 days old. Camera lucida drawings, × 1027

On raspberry cane plugs, cultures eighty days old; conidia taken from pseudopionnotes:

Conidia: 2–septate, rare
3–septate, 66 per cent, 41.4 x 5 (32–48 x 4–5.8) $\mu$
4–septate, 34 per cent, 49.3 x 5 (44–56 x 4–5.8) $\mu$

On potato agar containing one per cent glucose, cultures twenty-two days old; conidia from pseudopionnotes:

Conidia: 2–septate, 3 per cent, 37.7 x 4.4 (36–40 x 4–5.3) $\mu$
3-septate, 83 per cent, 43.5 x 5.2 (33.3–56 x 4–6.6) $\mu$
4–septate, 14 per cent, 52.3 x 5.4 (42.6–60 x 4.6–6.6) $\mu$

On slightly acidified hard potato agar, cultures eleven days old; conidia from pseudopionnotes:

Conidia: 3–septate, 24 per cent, 48.7 x 5.3 (35.3–53.3 x 4.6–6.6) $\mu$
4–septate, 76 per cent, 52.9 x 5.5 (46.6–56 x 4.6–8) $\mu$
5–septate, rare

On potato plug, cultures eighty-three days old; conidia from pseudopionnotes:

Conidia: 2–septate, rare
3–septate, 76 per cent, 43.5 x 5.2 (36–48 x 4–8) $\mu$
4–septate, 24 per cent, 46 x 5.5 (42–49.3 x 4.6–6.6) $\mu$

On synthetic agar,[4] cultures thirty-three days old; conidia from pseudopionnotes:

Conidia: 3–septate, 24 per cent, 50.7 x 5.1 (41.6–58.5 x 4.5–6.5) $\mu$
4–septate, 76 per cent, 54 x 5.2 (29.9–59.8 x 3.9–6.5) $\mu$
5–septate, rare

## NOMENCLATURE

The name *Fusarium martii* was first used by Appel and Wollenweber (1913) to describe a fungus which they regarded as identical with *Fusisporium solani* Martius. These investigators presented a detailed description of the species, as did also Sherbakoff (1915 b) a few years later in his monograph on the Fusaria of potatoes. In both instances the fungus

[4] Richard's solution with two per cent agar.

was found on decaying potato tubers and was considered to be saprophytic on that host. On the other hand, Carpenter (1915) refers to a culture of *Fusarium martii* isolated from *Pisum sativum* by Westerdijk and determined by Wollenweber, which evidently was considered to be parasitic since it was thought by Miss Westerdijk to be *F. vasinfectum* var. *pisi* Van Hall, the cause of the St. John's sickness of garden peas. So far as is known, no inoculation experiments were made. Wollenweber shows drawings of this strain in *Fusaria autographia delineata*, issued in 1916.

The fungus isolated from diseased bean roots, and proved to be parasitic on this host, is practically identical with *F. martii*. The spore measurements are approximately the same. The color production is identical with that of *F. martii* and the pathogene in appearance agrees remarkably well with the plates given by Carpenter (1915). The number of septa in the conidia, and the proportion of conidia having the same number, also are similar. One slight difference was observed. Appel and Wollenweber state that 5-septate spores are rare, but they find a sufficient number to give spore measurements and drawings. Sherbakoff likewise finds as many as seven per cent of 5-septate spores on some media. In the species under consideration, 5-septate spores were found in less than one per cent. The fact that they occur in fewer numbers, however, seems of small consequence and can scarcely be pointed to as a distinct difference in the two organisms. Moreover, a culture of the fungus from affected bean roots was sent for determination to Dr. Sherbakoff, who states, in a letter to the writer, that this fungus "is morphologically the same as *F. martii* because of the same macroscopical characters, the same type and size of conidia and of the same chlamydospores." Slight differences that might occur he considers not sufficient to separate this fungus from the above species.

For comparison of the fungus under consideration with *F. martii*, cultures of the latter were obtained at various times from several different sources. The first culture received was from R. J. Haskell and was originally from Dr. Sherbakoff, the latter having discarded his own cultures; a second culture was supplied by the Bureau of Plant Industry from Wollenweber's collection; a third was from J. Westerdijk at the Centralstelle für Pilzkulturen. The macroscopical appearance of subcultures from these were slightly different from the organism from bean root. There was also a slight difference in appearance among the three

strains of *F. martii*. The difference lay in intensity of color, greater or less amount of aerial mycelium, and variations in the formation of pseudopionnotes. Spore measurements made from the culture obtained from the Wollenweber collection varied considerably from the measurements given by Appel and Wollenweber and by Sherbakoff. The cultures from the Centralstelle für Pilzkulturen, however, agreed very closely with the original measurements. Unfortunately the strain isolated from potato by Dr. Sherbakoff was lost before spore measurements could be made. Inoculation experiments, however, were conducted with all three strains with the bean as the host plant. In no case did infection occur. It is very improbable that these negative results are due to unfavorable conditions, as positive results were always obtained at the same time with the fungus from bean roots. There is no evidence that *F. martii* is parasitic on the bean root.

From the foregoing statements it seems scarcely possible that the bean Fusarium is identical with *F. martii*. There is a distinct physiological difference, and possibly slight morphological differences. The latter are so unimportant that the writer does not feel justified in using them as the basis of a new species or even a new variety. Physiological differences, however, have been used in this genus as the basis of new varieties. *Fusarium vasinfectum* var. *inodoratum* Wr. differs from *F. vasinfectum* Atk. only by the absence of odor. On the other hand, in other groups it has been the custom, when the physiological difference was one of pathogenicity, to treat the new form as a biologic species. For this reason the writer has used the trinomial *Fusarium martii phaseoli*.

Since one strain of *F. martii* was isolated from a diseased pea root by Dr. Westerdijk, there is the probability of another biologic species, *F. martii pisi*. The writer, however, obtained no infections on the garden pea when inoculations were made with *F. martii*. The original species appears to be saprophytic.

## LIFE HISTORY

The time of bean planting in New York State varies according to weather conditions, but usually the seed is put into the ground in the first half of June. The soil at that time is in a warm and moist condition. Thus as soon as germination of the bean seed takes place, external factors are favorable for the infection of the young roots by the dry

root-rot fungus. The taproot, being the first to develop, soon shows symptoms of the disease. This is frequently a week or two after the host plant is above ground. It has been determined by experiment that further infections may take place at any time during the growing season of the bean plant.

The exact mode of infection is not known. The fungus, however, may penetrate the healthy epidermis. After the mycelium has once

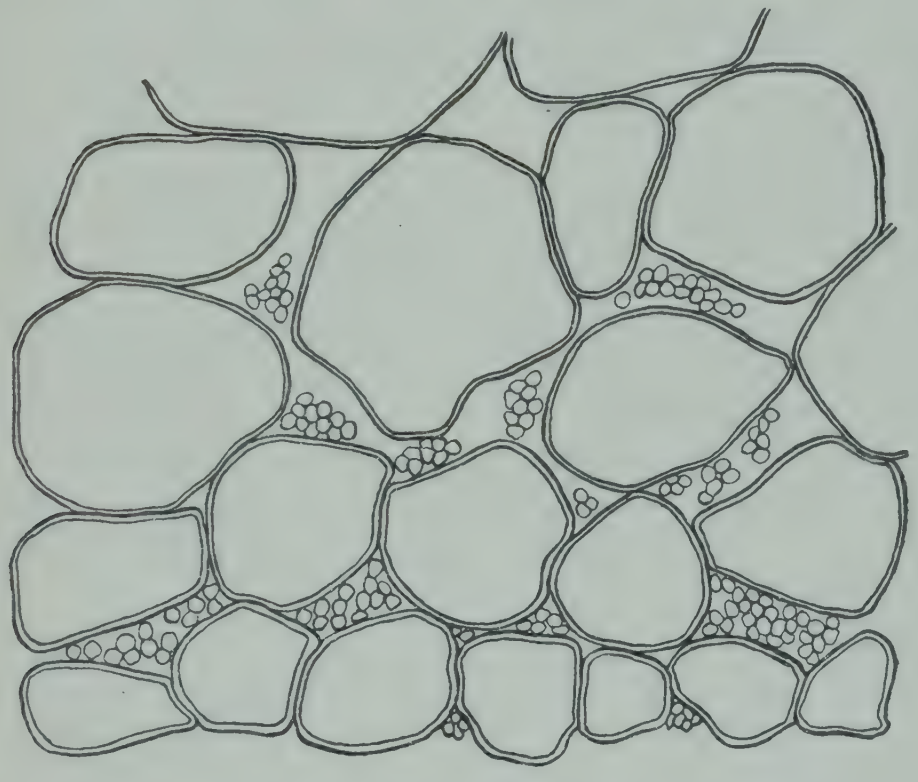

FIG. 135. CROSS SECTION OF THE CORTEX AND EPIDERMIS OF THE TAPROOT OF A BEAN AFFECTED WITH DRY ROOT-ROT

An early stage in the progress of the disease, showing the intercellular and parallel hyphae. Camera lucida drawing, × 514

gained entrance to the host, it is for a short time intercellular in the cortical tissue. In the main the hyphae are found extending longitudinally with the taproot. Occasionally as many as a dozen hyphae may be observed growing parallel in the intercellular spaces (fig. 135). This tendency on the part of the fungus to form rhizomorph-like structures is further developed on the outside of the host, where strands 75 $\mu$ in diameter frequently occur over the diseased areas. Likewise, in culture,

*Fusarium martii phaseoli* produces these strands, which at times develop into coremium-like structures of fructification.

The mycelium in the host rarely extends any distance above the surface of the soil. In its growth in the cortex it possibly reaches its greatest height; here, at times, the coloration due to the fungus may appear on the lower part of the stem. The mycelium in the cortex of the upper part of the root does not penetrate into the vascular bundles, hyphae having been observed to enter the vascular system only through the small lateral rootlets on the lower part of the taproot. The mycelium does not long remain intercellular, but soon enters the cells of all the tissue. From the lower part of the taproot the hyphae progress upward through the cells of the vascular system. Frequently they fill these cells or cause them to collapse, but seldom is a wilting of the host plant produced. The growth of the fungus is extremely slow; by harvest time of the host it frequently has not reached within an inch of the surface of the soil. The height that it attains in the vascular tissue, however, depends on the time of infection.

*F. martii phaseoli* produces two kinds of spores on and in the bean roots. They are the chlamydospores and the conidia of the fungus. The chlamydospores are borne singly, or, less frequently, in small chains within the host tissue. For the most part they are found in the cortex. In the smaller fiber-like rootlets they occur in greater numbers than in the larger lateral roots and in the taproot. This is due probably to an absence of sufficient food material in the smaller roots. Repeated attempts to germinate these spores have failed. Evidently the optimum set of conditions governing germination has not been discovered. Conidia are rarely produced in abundance on the host during the growing season. Frequently spores cannot be found even on severely diseased roots. Before the cause of the dry root-rot was determined, many specimens of infected bean roots were examined without success in finding the spores of the causal organism. A few instances only have been observed of large production of conidia on the dead parts of affected roots. Such cases were during rainy weather, and then the production was so great that the roots appeared whitish. Apparently a sufficient number are always produced for the dissemination of the fungus. In many of the infested fields a small quantity of soil will contain the pathogene to such

an extent as to cause immediate infection of bean seedlings. This, however, might be due to the mycelium.

From observations it appears that as a rule the fungus is disseminated in the manure used to fertilize the bean fields. It is the practice of growers to pull the bean plants in the late summer, and, after threshing the seed, to use the remainder of the plant as bean straw. This is fed to cattle and sheep and is one of the valuable by-products of the bean industry. The straw contains the diseased bean roots, which are seldom eaten but are thrown into the compost heap where they undergo further decomposition. The fungus here lives saprophytically and produces its spores on old bean roots and stems. When the manure is spread over the fields the pathogene also is carried to new areas. A striking instance of this was observed on a farm near Perry, New York. During the latter part of the growing season of 1916, the location could be determined where four loads of manure had been distributed in the bean field. This was due to the fact that the dry root-rot was more severe in these places.

In the sections where snap beans are grown, this method of dissemination of the fungus does not apply. Here, after the crop is harvested, the vines are plowed under, not pulled for straw. Thus the fungus does not get into the manure, and therefore is not distributed so readily over the fields.

The pathogene may be carried from one field to another in various other ways. It may be disseminated on the feet of horses and of men, and on tillage instruments. It may be spread by the wind, blowing dust from field to field. Observations in the greenhouse indicate that it can be carried by insects. Another means of dissemination is by washing. In the valleys about Warsaw and Attica, New York, all the fields are equally contaminated with *F. martii phaseoli*, whether or not they have been planted to beans or have had bean-straw manure applied to them. It is known, however, that in certain years these fields have been under water during the early spring. At such periods it is very probable that the pathogene is carried from field to field along the valleys.

There are no indications that the fungus is carried with the seed, although if the seed is not well cleaned it may harbor small pieces of the diseased roots and particles of dirt containing the pathogene.

The dry root-rot fungus may overwinter in the bean straw or in the compost heap, and in the following spring it is returned to the fields.

This is a common method of hibernation, but it does not account for the presence of the fungus in the majority of fields in the bean section of New York State. The pathogene when it once gains entrance into a field is very persistent, and may live for a number of years as a saprophyte in the soil. Since the common practice in the bean section is a three-years rotation, the fungus is known to exist for such a period in the absence of the host plant. Observations indicate further that it may live for as long a period as ten years. In the laboratory, in soil to which no moisture was added, the pathogene died within a period of two years. In addition to water, decaying organic matter is no doubt necessary for the persistence of the pathogene in a saprophytic condition.

Only one experiment has been conducted which has any bearing on the length of time the pathogene may live in the soil under natural conditions. This experiment was begun in 1915 and data were taken at the end of three years. Four rows of beans, approximately 100 feet long, were inoculated with the fungus *F. martii phaseoli*. Four rows were planted as a check to determine whether the pathogene was already inhabiting the soil. The plants of the check rows remained healthy. At the end of the season the bean plants were cut off and the roots were allowed to remain in the soil. The plot was then dragged over and sown to wheat and clover, both red clover and alsike (*Trifolium pratense* and *T. hybridum*) being used in the seeding. After the wheat was cut in 1916, the clover remained on the plot until the spring of 1918, when the plot was planted to potatoes. In October of 1918 soil was taken from the plot where the diseased plants had been, and was placed in sixteen pots in the greenhouse. Three seeds of the Red Kidney variety of beans were placed in each pot. At the end of five weeks the roots of the plants were examined. In no case were lesions of the dry root-rot observed on them. The results of this experiment are contrary to all observations of the writer in the field. Moreover, the test is small and inconclusive, and is given here merely for what it is worth.

In just what form the pathogene persists during the winter and in the absence of its host plant has not been determined. It is probably in the mycelial stage during favorable conditions and in the chlamydospore stage during adverse conditions. Repeated examination of overwintered matter has never revealed the presence of a sexual stage.

## PATHOGENICITY

### *Inoculation experiments with the bean plant*

Many hundreds of inoculations have been made from time to time with *Fusarium martii phaseoli* on the roots of bean plants. In approximately one hundred per cent of the tests, infections occurred. These experiments were conducted both in the greenhouse and in experimental gardens. Infection takes place readily when the soil is contaminated before the seed is planted, when the seeds are dipped in suspensions of spores from a pure culture and planted in sterilized soil, and when inoculations are made with the pathogene after the plants are above ground. The incubation period under favorable conditions is about five days to a week. The spores used in these experiments were taken from pure cultures and always showed a high percentage of germination. The age of the cultures varied greatly; this factor, however, is unimportant, since the spores do not lose their viability very early.

Inoculation experiments were conducted to determine other important points respecting the pathogenicity of the fungus. The length of the period of susceptibility in the bean plant was thought to be worthy of consideration. It was believed that if it were found that infection takes place only in the seedling stage, a basis for controlling the disease would be available. It might be possible to protect the bean roots from the pathogene for a short time. On the other hand, the extermination of the fungus in the soil is exceedingly difficult without injury to the host plant or without too great expense. It was found, however, that the bean plants were susceptible over a greater period than the seedling stage. The results of the experiment to determine this point are set forth in table 1. The seeds used in the experiment were of the White Marrow variety.

The plants inoculated thirty-one days after planting became infected as readily as did those inoculated at the time of planting. From this it is evident that the period of infection does not extend over the seedling stage only, but on toward the maturity of the plant. It is possible that the plants are susceptible throughout their period of life. Early infection, however, would be more severe, as the fungus grows but slowly in the host.

TABLE 1. RESULTS OF AN EXPERIMENT TO DETERMINE THE PERIOD OF SUSCEPTIBILITY OF THE BEAN PLANT TO FUSARIUM MARTII PHASEOLI

| Date of planting (1915) | Number of days until inoculation | Number of plants | Number of infections |
|---|---|---|---|
| July 14 | None | 33 | 33 |
| July 30 | Check | 35 | 0 |
| July 30 | 8 days | 40 | 40 |
| July 30 | Check | 40 | 0 |
| July 30 | 16 days | 40 | 39 |
| July 30 | Check | 45 | 0 |
| July 31 | 31 days | 36 | 36 |
| July 31 | Check | 36 | 0 |

An experiment was conducted to determine whether the pathogene can live over winter in the compost heap and be carried back to the land. For this experiment manure was procured from a sheep barn where bean straw had been fed. The experiment was run in duplicate, one plot being at Perry and one at Ithaca. It is frequently almost impossible in certain counties to obtain land free from this pathogene. Since Ithaca is out of the bean-growing district, it was more or less certain that the land there would not be contaminated with the fungus. The experimental plot at Perry was situated in the center of an old apple orchard and also proved to be free from the organism.

In each plot two rows of beans, of approximately 150 plants each, were used. In some instances the seed-corn maggot (*Phorbia fusciceps* Zett.) and the slug (*Agriolimax* sp.) destroyed a number of plants. One row

TABLE 2. RESULTS OF AN EXPERIMENT TO DETERMINE WHETHER FUSARIUM MARTII PHASEOLI MAY WINTER IN THE COMPOST HEAP AND BE CARRIED BACK TO THE LAND THE FOLLOWING SEASON

| | Number of healthy plants | Number of diseased plants |
|---|---|---|
| Plots at Ithaca | | |
| Treated row | 47 | 40 |
| Check row | 147 | 2 |
| Plots at Perry | | |
| Treated row | 38 | 107 |
| Check row | 96 | 3 |

was used as a check row, while the other was heavily fertilized with the bean-straw manure. The manure contained decaying pieces of bean stems and roots which had been in the compost heap during the preceding winter. The plots at Ithaca were planted on June 22, 1916, and those at Perry were planted on June 28, 1916. The results of the experiment are shown in table 2.

The few diseased plants appearing in the check rows can be accounted for readily as infections caused by washings from the diseased rows. The fungus also could have been transferred during cultivation.

### *Cross-inoculations*

Many inoculation experiments were conducted to find other hosts of *Fusarium martii phaseoli*. These experiments were conducted both in the greenhouse and in the garden. In all cases rows of beans were inoculated with the pathogene as a check. Without exception infection was obtained on the bean. The following plants proved susceptible to *F. martii phaseoli*: the tepary bean (*Phaseolus acutifolius* Gray var. *latifolius* Freeman), the scarlet runner bean (*P. multiflorus* Willd.), the adzuki bean (*P. angularis* Willd.), the moth bean (*P. aconitifolius* Jacq.), the Black-eye cowpea (*Vigna sinensis* [L.] Endl.), and the kulti bean (*Dolichos biflorus* L.). Infection was very light on the scarlet runner and the lima bean.

Negative results were obtained with a number of legumes and other plants. This list is as follows: the garden pea (*Pisum sativum* L.); the field pea (*P. sativum* L. var. *arvense* Poir.); red clover (*Trifolium pratense* L.); alsike clover (*T. hybridum* L.); vetch (*Vicia* sp.); the following varieties of soybeans (*Soja max* Piper)— Medium Green, Ito San, Auburn, Wilson; corn (*Zea mays* L.); potato (*Solanum tuberosum* L.); oats (*Avena sativa* L.); wheat (*Triticum* sp.); and the following weeds —*Ambrosia artemisiifolia* L., *Prunella vulgaris* L., *Chenopodium album* L., *Rumex* sp. The weeds used in the inoculation experiments were those found commonly in the bean fields.

## EFFECT OF WEATHER CONDITIONS

In the case of root parasites, infection is not so dependent on weather conditions as with those pathogenes which attack parts of plants above ground. Such factors as sun, wind, rain, and dews are eliminated.

Except under very prolonged drought there is sufficient moisture in the soil for spores to germinate and infect the host. Temperature appears to be the chief limiting factor, and from recent articles on the subject this varies greatly with the pathogene and the host. Gilman (1914 and 1916) considers high temperature favorable to infection of cabbage by *Fusarium conglutinans* Wr. Tisdale (1917 a) came to similar conclusions in his observations on the infection of flax by *Fusarium lini* Bolley, and states that from 15° to 16° C. is the minimum temperature at which infection will occur. Ramsey (1918), on the other hand, is of the opinion that a cool, moist soil is essential for infection by *Spongospora subterranea* (Wallr.) Johnson to occur on potato tubers.

In working with *Fusarium martii phaseoli*, the organism under consideration, Reddick (1917) found that infection occurred between temperatures of 15° and 34° C. His results have been substantiated by the writer. These temperatures include, with the exception of a few cases, the limits of the soil temperature found to exist at Perry, New York, during the growing seasons of 1916 and 1917. Records were taken at that place with a continuous self-recording soil thermograph. In no case was the temperature recorded higher than 30° C., and only a few times did it drop below 15° C.; in the latter instances it always rose immediately. From these data it is apparent that the soil temperature about Perry, which is near the center of the bean district, is always sufficient for the bean plant to become infected with *F. martii phaseoli*.

Besides the effect that soil temperature has on infection, there is also its effect on the progress of the disease after infection has once taken place. The latter is possibly of the greater importance. The problem here is more complex and very few definite conclusions have been drawn pertaining to it. Reddick, in the article cited above, has shown that soil temperature influences very greatly the growth of the bean plant. High temperatures allow much more rapid yet healthy growth than do low temperatures. Thus it is difficult to analyze data concerning the effect of the disease at different temperatures of the soil, since the rate of growth of the host plant varies so much. There were, however, in experiments conducted under these conditions, indications that the disease is more severe at a soil temperature of 22° C. than at 34° C. The former temperature is nearer the average of the soil temperature found in the bean district during the growing seasons of 1916 and 1917.

Even more marked than the effect of soil temperature on the disease is the effect of varying amounts of soil moisture. As already stated, the pathogene *F. martii phaseoli* is not a wilt-producing organism although the mycelium frequently invades the vascular system. The effect of the fungus is rather to kill and dry up the tissue as it progresses up the root, thus greatly reducing the root system of the plant. The roots that remain healthy or are able to carry on their normal functions are the surface roots. If there is an abundance of water in the soil, these surface roots can supply the plant with sufficient moisture. As the percentage of soil moisture decreases, however, this ability of the surface roots to supply moisture also decreases. A drought of ten days or two weeks will bring forth from the growers the statement that their beans are "going back." The expression is descriptive. The symptoms of the disease become very evident in a relatively short time. If a prolonged dry spell occurs at the time of blossoming and pod production, it is very injurious to the diseased plants. The yield, without doubt, will be reduced over fifty per cent. On the other hand, a very high moisture content of the soil aids materially in the dissemination of the fungus. Moisture also causes a more rapid progress of the disease in the host, since the diseased parts, which are usually dry, absorb water very readily. In this way sufficient moisture is supplied to the pathogene. A continuous rainy season, however, does not cause a noticeable reduction in yield of diseased plants. During the season of 1915 a field of White Marrow beans near Wyoming, New York, was under the observation of the writer. The plants on this field were severely infected, and at podding time fifty per cent or more of their root system was destroyed. Nevertheless a yield of 24 bushels to the acre was produced. Unquestionably this was due to the fact that the surface roots, which are more numerous in damp than in dry soil, were able to supply the plant with water. During the dry season of 1916 the writer observed numerous bean fields affected with the dry root-rot which did not produce over two or three pods to a plant. In this season there was sufficient moisture directly after planting time to cause a succulent growth in the plant and a rapid progress of the disease. Throughout the dry period that followed, the plants were checked in their growth and few pods were formed.

## EFFECT OF DRY ROOT-ROT ON THE YIELD OF THE BEAN CROP

Few experiments have been conducted to determine the exact effect of any plant disease on the yield of its host. For a crop that is subject to numerous diseases, such information is frequently of extreme value. This is true of the bean, in the case of which several pathogenes may occur on the roots of the plants. One of these is the dry root-rot, and, since inoculations can be controlled, an experiment to learn the effect of this disease on the bean crop can readily be conducted.

Since the black root-rot is so frequently associated with the dry root-rot, it was considered advisable to determine the loss in yield resulting from each as well as from a combination of the two diseases. For the sake of accuracy such an experiment should be repeated through several seasons in order to avoid the effect of unusual weather conditions. A preliminary experiment of this type was conducted in 1916. The seed was not planted until July 20, and therefore the crop did not mature before the early frost of that season. Plants in the rows inoculated with *Fusarium martii phaseoli* were considerably dwarfed, but those inoculated with *Thielavia basicola* could not be distinguished from the check rows. A combination of the two, from all appearance, caused no more injury than did *F. martii phaseoli* alone. It was unfortunate that the beans could not be harvested, inasmuch as the weather was especially favorable for the effects of the disease to appear in the yield.

In 1917 a more extensive experiment was conducted at Ithaca. The weather conditions were very unfavorable for the dry root-rot, but were advantageous for the bean plant. Marked losses, therefore, which would be noted in average years or in years favorable for the disease, were not obtained. Some interesting facts appeared in the experiment, and for this reason the data, although incomplete, are set forth here.

The plot at Ithaca used for the experiment was located on a low piece of ground. The soil was a gravelly loam. In previous years the plot had been in alfalfa, and no records show that it had ever been planted to beans. It was likewise out of the bean area and the soil proved to be free from the pathogene *Fusarium martii phaseoli*. The soil was likewise free from *Thielavia basicola*, since all checks remained healthy even though this organism is widely distributed and occurs on such hosts as alfalfa.

The plan of the experiment was as follows: Plants in row 1 were inoculated with *Thielavia basicola*; row 2 remained as a check; row 3

was inoculated with *T. basicola* and *Fusarium martii phaseoli*; row 4 was a check; row 5 was inoculated with *F. martii phaseoli*; row 6 was a check. The rows were three feet apart and one hundred feet long. They were repeated five times. To eliminate outside rows, buffer rows were planted on either side of the plot.

The seed, which was a Marrow Pea variety, was planted on June 14. Rain had fallen on the preceding day and the soil contained sufficient moisture to keep the spores of the fungi from being killed by drying. The same quantity of seed was used for each row, and all seeds were inoculated with the legume bacteria before planting. The check rows were covered before the others were inoculated, to avoid any danger of contamination.

During the summer the plot was cultivated twice and weeded, but it was not hoed. Thus there was little danger of the fungi's spreading from the infected rows to the check rows. When the plants were pulled in the fall no infection was found to have occurred on the check plants.

Since the season was wet and the plots were located in the low ground, plenty of moisture was retained in the soil. After June 14 rain fell on the following dates: June 15, 18, 19, 20, 23, 26, 27, 28, and 29 — a total precipitation of 3.89 inches. During July rain fell on the following dates: July 1, 2, 3, 4, 6, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20, 21, 26, and 29 — a total precipitation of 3.25 inches. In the month of August rain fell on the following days: August 2, 3, 6, 8, 9, 10, 13, 14, 15, 16, 22, 23, 28, 29, and 30 — a total precipitation of 8.45 inches. In the first half of September there was precipitation on the 1st, 2d, 6th, 7th, 8th, 9th, and 10th, with a total of 1.41 inches. Thus it may be seen that the soil was in a moist condition throughout the summer, especially during the critical month of August when the pods are produced. The plants grew rapidly and soon covered the ground. The majority produced a large number of pods, and from the general appearance the inoculated rows could not be distinguished from the check rows.

When the plants were pulled in the fall, considerable injury was observed on the roots of the plants inoculated with the dry root-rot fungus. In many cases all that remained of the roots was a dried stub, but the parts above ground were apparently healthy. The rows affected with the black root-rot showed more injury than during the dry, hot summer of 1916. Few plants, however, showed serious injury. Those

inoculated with both the fungi could not be separated from those inoculated with *Fusarium martii phaseoli* alone. As to the yield in the different rows, nothing could be determined from observation. Each row was harvested and threshed separately and the amount of seed was weighed. The data are given in table 3:

TABLE 3. EFFECT OF ROOT DISEASES ON THE YIELD OF THE BEAN DURING THE SEASON OF 1917

| Row | Inoculation | Weight of seed (grams) | Reduced or increased yield (per cent)* |
|---|---|---|---|
| | Buffer row | | |
| 1 | Black root-rot | 3,585 | 72.6 |
| 2 | Check | 4,938 | |
| 3 | Dry root-rot<br>Black root-rot | 3,749 | 76.4 |
| 4 | Check | 4,877 | |
| 5 | Dry root-rot | 4,743 | 105.9 |
| 6 | Check | 4,083 | |
| 7 | Black root-rot | 4,843 | 107.4 |
| 8 | Check | 4,933 | |
| 9 | Dry root-rot<br>Black root-rot | 3,538 | 72.9 |
| 10 | Check | 4,778 | |
| 11 | Dry root-rot | 3,751 | 81.0 |
| 12 | Check | 4,483 | |
| 13 | Black root-rot | 4,722 | 100.5 |
| 14 | Check | 4,916 | |
| 15 | Dry root-rot<br>Black root-rot | 3,759 | 75.8 |
| 16 | Check | 5,006 | |
| 17 | Dry root-rot | 4,781 | 96.3 |
| 18 | Check | 4,922 | |
| 19 | Black root-rot | 4,565 | 101.1 |
| 20 | Check | 4,111 | |
| 21 | Dry root-rot<br>Black root-rot | 3,915 | 92.6 |
| 22 | Check | 4,345 | |
| 23 | Dry root-rot | 4,242 | 105.0 |
| 24 | Check | 3,738 | |
| 25 | Black root-rot | 2,421 | 58.0 |
| 26 | Check | 4,604 | |
| 27 | Dry root-rot<br>Black root-rot | 2,810 | 65.0 |
| 28 | Check | 4,041 | |
| 29 | Dry root-rot | 3,394 | 82.7 |
| 30 | Check | 4,162 | |
| | Buffer row | | |

* The reduced or increased yield is calculated by determining the percentage of yield of the diseased row in relation to the average of the yields of the two adjacent check rows.

In studying this table several points should be taken into consideration which have or might have a disturbing effect on a proper interpretation of the data. In all instances these points deal with individual rows. Since the first row served as a buffer, the yield was not determined, and hence the check percentage of row 1 was calculated from only one check row. In all other cases the average of the check rows on both sides of the diseased row was used. In check row 6 it may be seen that the yield was far below the normal. The cause of this is unknown. It resulted, however, in unfair calculated check percentages for rows 5 and 7. If rows 4 and 8 only had been used, the check percentages would not have been above one hundred. Row 25, which shows a very low yield and therefore a low check percentage, had a small number of plants. Row 27 also had a small number of plants, but this was not evident on the yield. The writer appreciates the fact that rows of equal length may have varying numbers of plants without affecting the yield of these rows. For this reason it is considered best to use rows in an experiment of this type instead of a certain number of plants. Just how much thinning a row may permit before a noticeable decrease in yield occurs is not known.

In consideration of these disturbing factors, very few data are presented which show that the black root-rot reduces the yield of beans to any extent. The weather, no doubt, was as favorable as possible for this disease and the root-rot approached its maximum in severity. The injury from the black root-rot was brought about to a large extent by the destruction of the plants in the seedling stage. The remaining plants, therefore, had a better opportunity to develop and offset this injury. The calculated check percentages for the dry root-rot on the whole are high. This is to be expected, however, when the soil retains a large amount of moisture throughout the growing season. With the combination of the diseases there appears to be a consistent reduction in the yield.

A further experiment to determine the effect of the dry root-rot on the yield of the bean was conducted during the season of 1918. The plot of land selected, although not so advantageous for beans, was located on higher ground than that used in the experiment of 1917. The soil contained a considerable amount of clay. The plan of the experiment was the same as in 1917 with the exception that only the fungus *Fusarium*

*martii phaseoli* was used. Six rows were inoculated, with a check row left between each two treated rows. All seed used in the experiment was inoculated with the root-nodule organism.

During the summer the plot was cultivated twice and weeded. At podding time a slight difference could be distinguished between the check rows and the rows of infected plants. That this should occur in 1918 and not in 1917 was due to the lower ground on which the plot was located in 1917 and to the general raininess and cloudiness of that growing season. The plot was planted on June 4, after which rain fell on the following dates: June 6, 7, 10, 11, 12, 13, 14, 21, 22, 23, 25, 28, and 29 — a total precipitation of 3.05 inches. Thus a sufficient amount of soil moisture was present during the infection period. In July rain fell on the following dates: July 1, 3, 5, 9, 10, 11, 17, 24, 29, and 30 — a total precipitation of 4.55 inches. During August, when the pods are formed, there was less than half as much precipitation as in the month of August, 1917; rain fell on the following dates: August 4, 5, 8, 10, 14, 24, 26, 28, 29, and 30 — a total precipitation of 3.76 inches. The plants were harvested in the first part of September. The results of this experiment are shown in table 4:

TABLE 4. EFFECT OF THE DRY ROOT-ROT ON THE YIELD OF THE BEAN DURING THE SEASON OF 1918

| Row | Inoculation | Weight of seed (grams) | Reduced yield (per cent)* |
|---|---|---|---|
| 1 | Check | 291 | |
| 2 | Dry root-rot | 548 | 61.9 |
| 3 | Check | 1,478 | |
| 4 | Dry root-rot | 723 | 47.9 |
| 5 | Check | 1,538 | |
| 6 | Dry root-rot | 954 | 56.3 |
| 7 | Check | 1,848 | |
| 8 | Dry root-rot | 709 | 43.8 |
| 9 | Check | 1,392 | |
| 10 | Dry root-rot | 720 | 61.7 |
| 11 | Check | 941 | |
| 12 | Dry root-rot | 484 | 51.4 |

* The reduced yield was calculated as in table 3 (page 1024).

The experimental plot used in 1918 was an apparently level piece of ground, nevertheless it may be seen that the yield near the center was

much higher than that on either side. However, observation in most bean fields will show that the outside rows are composed of low-yielding plants. In other respects the data for this experiment are not difficult to analyze. Weather conditions were such as to make the effect of the dry root-rot very noticeable. The decrease in yield in diseased rows averages approximately fifty per cent.

## CONTROL

### ROTATION OF CROPS

Since the cause of the dry root-rot is a soil pathogene, the possibility of controlling the disease through longer crop rotations was considered very early in these investigations. The common rotation practiced by the growers of dry shell beans is but three years, and frequent instances are found in which the rotation is only two years. It is customary to follow beans with wheat and then clover, although in the fruit-growing districts this rotation may vary somewhat. In all localities, however, a few growers vary their rotations considerably. For this reason a survey was made in Wyoming County in 1915, and in Genesee, Livingston, and Monroe Counties in 1916, to determine whether these variations in rotation affect the disease to any extent. Very little information was obtained. Fields were observed in which beans had not been grown for ten years and yet the dry root-rot was present. In some of these fields the pathogene might have been continuously returned to the soil in the manure. On the other hand, this explanation could scarcely hold for pasture land.

One point drawn from the survey that should be noted is, the shorter the rotation the more serious is the disease, although long rotations do not eradicate the fungus. From this it appears that the pathogene will accumulate more rapidly in the presence of the bean plant. Nevertheless it still persists in the absence of this host plant, and, as far as is known, no other crop grown in rotation with the bean and no weeds found commonly in the fields are susceptible to its attacks. It would thus appear that the fungus lives saprophytically in the soil. It is not uncommon for pathogenic members of the genus Fusarium to do this, since they frequently have been isolated from the soil in the absence of their host plant. Pratt (1918) isolated *Fusarium radicola* Wollenw. and *F. trichothecioides* Wollenw., two potato pathogenes, from virgin soil in Idaho.

From the foregoing observations on the character of *Fusarium martii phaseoli*, it appears highly improbable that the dry root-rot of beans can be entirely eliminated by longer crop rotations.

### SOIL TREATMENT

The application of chemicals and fertilizers to the soil to destroy or hold in check soil pathogenes, has seldom proved successful on an extensive scale. In seedbeds and greenhouses where expense does not prohibit, treatment with formaldehyde may be used profitably. A formaldehyde solution applied in the furrow with the seed at the time of sowing has proved effective in the control of onion smut. On the other hand, the application of fertilizers has tended at times to lessen the effect of certain root diseases. Such has been the case in liming fields contaminated with the organism causing clubroot of cabbage. Acid phosphate applied to tobacco fields also has proved to be beneficial in holding in check the black root-rot.

During the season of 1915 a number of farmers near Perry and Warsaw, New York, under the direction of the Wyoming County Farm Bureau tried varying applications of lime and acid phosphate on their bean fields. Four of the farms were visited by the writer with H. M. Bowen, the County Agent, and careful observations were made. In no instance could it be determined that the fertilizers checked the disease to any extent. Similar reports were received from various other farms.

The application of toxic substances to the soil, especially non-volatile substances, must be made with great care. The roots of the plants are extremely sensitive and in the seedling stage great injury may be done to them. The pathogene, too, s frequently very resistant to chemicals and cannot be destroyed easily. Furthermore the after effects of treatment with various chemicals have been reported to be injurious to other crops grown in rotation. Sherbakoff (1915 a) has shown this to be true for clover when sulfur was applied previously; and Wheeler, Hartwell, and Moore (1899) have shown the same thing to be true for cereals.

However, regardless of the fact that clover generally occurs in the rotation with beans, a preliminary test was made with sulfur in the summer of 1915. Sulfur was drilled in with the seed at the rates of 200 pounds and 400 pounds to the acre. In neither case was the germina-

tion of the seed injured, but over 95 per cent of the plants showed severe infections of the dry root-rot. Later in the summer these rows were torn up and again planted to beans. It was thought that by that time the sulfur might have had an effect on the pathogene. Practically all the plants became infected. No further experiments with sulfur were conducted.

A volatile chemical which would kill the pathogene and then evaporate would be the ideal substance to apply. The use of formaldehyde possibly furnishes the closest approach to this condition. Calcium hypochlorite is another substance which would break down and leave no injurious substances. In the winter of 1915–16 preliminary tests were conducted with these two substances. One of the beds in the greenhouse was thoroughly contaminated with *Fusarium martii phaseoli*. It was then divided into three plots, each containing 12 square feet, and planted to beans. Plot 1 was treated with calcium hypochlorite applied at the rate of 200 pounds to the acre and drilled in with the seed; plot 2 was left as a check; plot 3 was treated with a formaldehyde drip similar to that used in onion smut treatment. The strength of the formaldehyde solution used was 1:100 and it was applied at the rate of 400 gallons to the acre. The germination of the seed was not injured by the formaldehyde, but injury to the extent of 75 per cent was observed on the plot treated with calcium hypochlorite. In both plots all plants were as severely infected as those in the check plot.

Further experiments with calcium hypochlorite and formaldehyde were conducted in the field in the season of 1916. A bean field near Perry, known to be contaminated with *F. martii phaseoli*, was used for the purpose. In each plot the beans were planted in four rows 28 inches apart, each row containing about 100 plants. Some of these were destroyed by the seed-corn maggot and by slugs. Plot 1 was treated with calcium hypochlorite at the rate of 200 pounds to the acre, the treatment being made ten days before planting; plot 2 was treated with the same substance at the rate of 100 pounds to the acre, and the chemical was drilled in at the time of planting; plot 3 was treated with formaldehyde, 1:100, which was applied as a drip at the time of planting at the rate of 400 gallons to the acre (this plot was repeated three times); in plot 4 the strength of the formaldehyde was doubled. Only in the last plot was any injury to the germination of the seed observed. No beneficial effects

were noted. In all plots, including the check, the proportion of healthy plants did not exceed 5 per cent.

Similar experiments were conducted in 1918 with the commercial preparation cyanamid. Three plots, each 20 feet long and 12 feet wide, were treated with varying amounts of the chemical, and a plot of similar size was used as a check. Plot 1 was treated at the rate of 50 pounds to the acre, plot 2 at 75 pounds to the acre, and plot 3 at 100 pounds to the acre. The applications were made at the time of planting, which was August 10, and the chemical was drilled in the rows. The variety of beans used was Well's Red Kidney. This method of treatment injured the germination considerably and retarded the growth of the plants to a severe extent. The experimental plots were examined on October 3. Over 90 per cent of the plants in the treated plots showed severe infection of the dry root-rot. No distinction could be made between these and the plants in the check plot. The results do not warrant further experiments with cyanamid.

### USE OF BEANS RESISTANT TO ROOT-ROT

Very little progress has been made in controlling plant diseases caused by soil-inhabiting fungi, except by the selection and development of disease-resistant strains. This is especially true when the pathogene concerned belongs to the genus Fusarium. Orton (1908) has used this method in checking the wilt of cotton, cowpea, and watermelon. Bolley (1903), and more recently Tisdale (1917b), have selected wilt-resistant varieties of flax. Jones and Gilman (1915) have employed the method with great success in controlling the yellows of cabbage. Norton (1914) and Edgerton (1918) have selected tomatoes resistant to the Fusarium wilt.

In New York State, fields of the White Marrow bean are frequently lacking in uniformity of type of the bean. Among the varying types is a strain to which, for convenience, the name *Flat Marrow* has been given by the writer. During the summer of 1915 it was observed that this strain exhibited a high degree of resistance to the dry root-rot.

In character the Flat Marrow varies somewhat, from a true White Marrow to a Burlingame (or Medium, as it is commonly called in New York State). The plant has a compact form of growth with broad and dark green leaves. The stems are heavier than in the common Marrow. The shape of the pod is that of a Medium, while frequent dashes of blue

lead to the belief that the strain is closely related to the Blue Pod Medium. The seeds are smaller and flatter than in the Marrow, but seldom are they the shape of those of the Burlingame. During the early part of the season these plants are difficult to distinguish from the Marrow, but a few weeks before harvest time they may readily be distinguished from the other varieties. This is due practically to the fact that the resistance to root-rot is remarkably noticeable (Plate LVI, 3). The Flat Marrow cannot be grown commercially in New York State, however, because of several objectionable characters. It is later than the White Marrow and, altho very productive, it frequently is injured by frosts. Another undesirable character is the length of its podding season. When the first pods are ripe the later ones are still small and green. Nevertheless its character of resistance to root-rot makes it a valuable bean.

It has been shown by the writer (1918) that resistance to anthracnose in beans can be transferred from one variety to another by hybridization. It was therefore hoped that by crossing the Flat Marrow with any of the common commercial varieties of bean, strains of the latter might be obtained resistant to the dry root-rot. In making selections among the Flat Marrow for parent stock, other characteristics besides disease resistance were considered. These were, earliness of maturing, and tendencies toward a White Marrow or a Medium type of bean. In 1915 only nineteen individuals were selected. The progeny of these were tested for resistance in the greenhouse during the following winter and in the field during the seasons of 1916 and 1917. Only seven strains were discarded. Numerous crosses have been made by the writer between the Flat Marrow and the White Marrow, and more recently E. W. Lindstrom and G. P. McRostie have hybridized the resistant type with a number of other commercial varieties of dry shell beans. The $F_2$ generation of all the first hybrids have been grown, and part of the $F_3$ generation. These have exhibited a very complex segregation, and it is the opinion of the writer that the character of disease resistance in this case is not governed by simple factors.

As yet no White Marrow strain has been isolated resistant to the dry root-rot. Insufficient knowledge concerning the genetical behavior of the characters of resistance to this disease, however, renders it impossible to state with certainty what may be done. Nevertheless it is hoped that desirable types possessing root-rot resistance may be obtained from the above crosses.

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CORNELL UNIVERSITY
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# THE INFLUENCE OF LOW TEMPERATURE ON SOIL BACTERIA

A. F. VASS

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# THE INFLUENCE OF LOW TEMPERATURE ON SOIL BACTERIA

# THE INFLUENCE OF LOW TEMPERATURE ON SOIL BACTERIA

A. F. Vass

Temperature is one of the most important factors influencing the growth and reproduction of microorganisms. Considerable work has been done in studying the effect of low temperature on the vitality and growth of bacteria, but the results have varied so greatly that it is difficult to draw any very definite conclusions from them. Certain investigators have found in frozen soils what they believed to be bacterial growth and reproduction to an even greater extent than is found at temperatures usually considered most favorable for protoplasmic activity.

The increased use of ice and the knowledge of water-borne epidemics have stimulated investigation in regard to the ability of the pathogenic bacteria to withstand freezing and storage in ice. In the work with pure cultures of pathogenic and nonpathogenic bacteria a great variation in results has been obtained. The natural ice dealer can find plenty of evidence to support his theory that the pathogenic bacteria in water are killed when the water is frozen and the ice stored for summer use. On the other hand, the public health officer can present equally strong evidence to show that the bacteria are not killed by freezing.

## HISTORICAL

The literature herein reviewed deals with the ability of the pathogenic and the nonpathogenic bacteria to withstand exposure to low temperature, the influence of low temperature on the bacterial flora of the soil, and the cause of the death of the cell upon exposure to low temperature together with the factors that influence it.

## PURE CULTURES

In the work with pure cultures both the pathogenic and the nonpathogenic forms were used. In some cases, however, there may be some doubt as to the purity of the cultures.

Regarding the resistance of bacteria to low temperatures, it was found by Schumacher (1874)[1], Göppert (1875), Frisch (cited by Pfeffer, 1903:238), Dewar and McHendrick (cited by Pfeffer, 1903:238), and Meyer (1900), that neither the spores nor the vegetative cells were killed by an exposure of several hours to temperatures ranging from −20° to −200° C.

Pictet and Yung (1884) exposed *Micrococcus lutea* and the vegetative cells of *Bacillus anthracis* to a temperature of −70° C. for one hundred and eight hours; this resulted in the death of the bacteria, as did also a temperature of −130° C. for twenty hours. The spores of *Bacillus subtilis*, *Bacillus anthracis*, and *Bacillus ulna* were not affected by the above-named temperatures. These results verified the conclusion of Melsens (1870), that long exposure of the yeast cells to −91° C. greatly decreases the fermentative activity. The enzyme of the yeast and the toxins of the poisonous bacteria were destroyed by exposure to extremely low temperatures. In his later work with microbes and diatoms, Pictet (1893) found that continued cold at −200° C. did not destroy these.

In studying the bacterial flora of snow, Janowski (1888) noted that continued low temperatures had very little effect on the bacteria. He found several hundred bacteria per cubic centimeter in water from snow.

Forster (1892) noted that the kinds of bacteria able to grow at 0° C. were not very numerous, but they seemed to be widely distributed, especially in water and on the surface and in the intestinal tract of both fresh- and salt-water fish.

In his work with *Bacillus anthracis*, Klepzoff (1895) noted that long exposure to low temperatures reduced the virulence of the organism and that the bacteria in blood and various organs were killed by exposing them to a temperature of −24° C. for twelve days. The colonies on agar plates were destroyed by exposing them for twenty-five days to the above-named temperature.

Kasansky (1899) exposed the pest bacillus and the diphtheria bacillus to temperatures ranging from −10° to −30° C. for five months and found that they were alive at the end of the experiment.

In their investigations with pure cultures of *Bacillus typhosus*, Sedgwick and Winslow (1900) found that from 30 to 60 per cent of the bacteria were destroyed during the first hour of freezing, and at the end of two weeks 99 per cent were destroyed. They studied the effect of alternate

[1] Dates in parenthesis refer to *Literature cited*, pages 1071 to 1074.

freezing and thawing, and noted that it was only slightly more harmful than continued freezing. Park (1901), in working with the same organism, found that all the bacteria were killed when embedded in ice for twenty-two weeks.

Macfadyen (1900) exposed bacteria to the temperature of liquefied air for twenty hours without its affecting their vital properties. The yeast-cell plasma also retained its peculiar properties to effect the production of carbon dioxide and alcohol. In a later report (1903) Macfadyen gives results from using liquid hydrogen, the temperature of this being −252° C. No appreciable effect on the bacteria was noted.

In studying the effect of the storage of ice on the bacteria contained therein, Sparks (1908) concluded that ice, even when cut from water which may contain pathogenic bacteria, is utterly incapable of passing on the disease if it is stored for some time before using. Similar results were obtained by Reudiger, who found that *Bacillus coli* was destroyed by storing in ice for eight weeks, and that the *Bacillus typhosus* organism was dead at the end of thirty-one days.

Budinov (1909) inoculated sterile milk with *Bacterium lactis acidi* and noted the effect of temperature on the life of the organism. At 30° C. most of the bacteria were dead in nine days, and at room temperature very few were alive at the end of eighteen days; while at 0° C. there was no change after thirty days. Alternate thawing and freezing had little or no effect. In such a case, however, temperature acts indirectly. The more favorable the temperature for growth, the greater is the production of acid, which in turn destroys the bacteria.

Poppe (1914) exposed the anthrax bacillus to a temperature of −16° C. for two weeks. The virulence and the reproductive capacity of the organism were not affected.

Jordan (1916) concluded that freezing had about the same effect as slow sand filtration, and that a great majority of the typhoid bacilli perish in a short time in ice, less than 1 per cent remaining alive after three weeks of freezing.

Hilliard, Torossian, and Stone (1915) noted, in their work with *Bacillus coli*, that 99 per cent of the organisms were killed by freezing in tap water for three hours; in the case of *Bacillus subtilis*, 80 per cent were killed under similar conditions. When the bacteria were placed in cream containing 30 per cent of butterfat, a protective action was noted.

Bartram (1916) exposed several of the disease-producing bacteria to winter temperatures for several months. Of the six cultures exposed, only two survived.

### SOIL FLORA

Among the early workers who studied the influence of temperature on the bacterial flora of the soil may be mentioned Remy (1902), who studied the seasonal variations. His quantitative study showed no great variation in the different seasons. No samples were taken during the winter.

A correlation between the number of bacteria in the soil and the moisture content was noted by Hiltner and Störmer (1903). Their results indicated also that there was a decrease in the total number of bacteria as the temperature of the soil was lowered. They noted, however, that certain of the frozen samples gave rather high results. Fabricius and Von Feilitzen (1905) found the same correlation to exist between temperature and the bacteria count. Their tests were made during the growing season.

Engberding (1909) concluded, from his studies of bacterial activity in fallow and cropped, and manured and unmanured, plots, that the moisture content was more important than the temperature. Most of his samples were taken during the period of plant growth. Of the two frozen samples studied, the counts were not so high as in some of the unfrozen samples, but they were sufficiently high to show that there are large numbers of bacteria in frozen soil.

Conn (1910) made a careful study of the bacterial flora thruout the year. He concludes from his results that quantitative determinations by means of the gelatin-plate method show that bacteria may be present in the soil in large numbers during the winter, and that there seems to be a rapid multiplication of bacteria in frozen soil. He noted that the number of bacteria increased and decreased nearly parallel with the moisture content of the soil in the frozen samples, but during the winter there was a striking exception to this. In a continuation of the above work (Conn, 1912) his earlier findings were confirmed. The same marked increase in number of bacteria in frozen soil, and decrease in thawed soil, was noted. The increase during the winter was thought to be due to the actual multiplication of the bacteria rather than to a mere rise of the organisms from lower depths brought about by mechanical forces alone.

Conn attempted to divide the soil bacteria into three classes — rapid liquefiers, slow growers, and Actinomyces. He found the greatest increase in the group of slow growers when the soils were frozen. In the quantitative work in the pure cultures he noted that certain types of soil bacteria occur thruout the year, while others apparently exist for short periods only and tend to recur at other times under similar conditions. He suggested the possibility that a different class of bacteria is in the ascendancy in winter from those which are benefited by the warm weather of summer; in which case the increase is not due directly to the low temperature, but to the depressing effect of the cold upon the group of bacteria which is able in summer to keep the winter bacteria in check.

Hutchinson (1911–12) noted that biological changes in the soil take place at a greater rate in the soils of India than in the European soils. The temperature of the India soils ranges from 25° to 30° C. during the growing season, whereas that of the European soils ranges from 16° to 18° C. At the lower temperatures ammonification and nitrification go on at the same rate, but in the soils of India there tends to be an accumulation of ammonia due to the increased activities of the ammonifying bacteria at the higher temperature.

The work of Conn was continued by Brown and Smith (1912) in their investigations of the bacterial activities of frozen soils. They made quantitative determinations of the number of bacteria in the soil during the fall, winter, and spring seasons. They noted a gradual decrease in the number of bacteria as the temperature was lowered. This decrease continued with more or less variation until March 1, when there was a marked increase. They suggested that their results confirm Conn's conclusion that bacteria are alive and multiply in frozen soils. They studied what they called the ammonifying, nitrifying, denitrifying, and nitrogen-fixing powers of frozen soils. These tests were made by inoculating 100 grams of an air-dry soil with a soil infusion representing five grams of the frozen soil to be treated. The nitrogenous materials added were stirred into the unsterilized soil by means of sterile spatulas. The authors conclude that frozen soils possess a much greater ammonifying power than do non-frozen soils, and that the ammonifying power of the soil increases until the temperature almost reaches zero, when a decrease occurs, and this is followed by a gradual increase which continues until the ammonifying power reaches its maximum at the end of the frozen period.

The nitrifying power of the frozen soils was weak and the ammonifying power was strong. The nitrogen-fixing power increased with the continuance of the frozen period, being independent of moderate changes in moisture conditions. In the fall the nitrogen-fixing power of the soil increased until the soil became frozen, when it almost ceased, after which a lesser nitrogen-fixing power was established.

Brown and Smith advanced the theory, which Conn suggested in an earlier publication, that the hygroscopic water in soils, remaining uncongealed, may serve as favorable media in which the bacteria may live and multiply to a comparatively large extent.

Czermak (1912) studied the changes in the so-called physical properties of soils resulting from their subjection to low temperature, high temperature, and the action of salts. He noted that when the soil colloids were coagulated by freezing, the soil surface and the hygroscopicity were reduced, and part of the nitrogen in the soil solution was absorbed, thus reducing the amount of available nitrogen. Alternate freezing and thawing increased the coagulation of the soil colloids. The length of time was more important than the intensity of the freeze. Hoffmann (1914), however, found little or no variation in the surface area of soils due to freezing.

Lyon and Bizzell (1913) studied the effect of freezing on the nitrifying power of the soil. They noted that freezing produced a soil favorable for nitrate formation. This was attributed to the beneficial effect of low temperature in overcoming the depressing influence of the crop previously grown.

Russell and Hutchinson (1913) offer an explanation very similar to Conn's to account for the increase of bacteria in frozen soils. They suggest that the protozoa may be the hostile organisms holding the bacteria in check in the unfrozen soils.

Conn (1914) verified in later studies what he had previously found, that the increase in bacteria in frozen soils is not due to the increase in moisture content which usually occurs in winter, and that the same increase may take place in potted soils where there is no possibility of the bacteria being carried up mechanically from lower depths during the process of freezing. He suggested the possibility that the increase may not be an actual multiplication but may result from the breaking up of the masses of bacteria by freezing. He considers this to be extremely

unlikely, however, for if such was the case the count following the thawing of the ground in the spring would not be so nearly the same as it was before the freeze. He attempted to explain this increase as due to a summer and winter flora but was unable to do so. There was a surprising similarity between the predominating types of bacteria found in different soils and in the same soil at different seasons.

In an attempt to explain the presence of large numbers of bacteria in frozen soils, Harder (1916) studied the effect of heavy frosts. He found that the number of bacteria in surface soil increased markedly after heavy frosts and maintained this high average during the winter months. Contrary to the findings of Conn and of Brown and Smith, Harder noted that the increase was directly related to the moisture content. His findings verified Conn's conclusion that the bacterial flora was more or less the same thruout the year, with the exception that after heavy frosts there was an increase in the proportion of small transparent colonies. Potted soils did not show this increase even when enriched with sugars. In fact the enriched soils showed fewer organisms in the frozen than in the unfrozen samples. Harder concludes that the increase in numbers was due to mechanical transportation by moisture coming up from below during heavy frosts.

Conn (1918), in his microscopic study of bacteria and soil fungi, found that there was more or less clumping of the bacteria on the soil particles, and in certain cases the organisms occurred in large sheets one individual thick. In practically all cases there was an increase in the individual count over the group count. In one table Conn gives the results of thirty-four groups and individual counts of soils made at different periods following the addition of manure. The results show that the individual count gives an increase of 50 per cent over the group count.

The findings of Brew and Dotterrer (1917) in their study of milk were very similar to those of Conn. Brew and Dotterrer noted a higher count with the microscope than with the plate method. The difference they attributed to the clumps of bacteria that do not break up on plating.

### MILK FLORA

Stiles and Pennington (1909), in their investigation with ice cream, found that the samples showed what seemed to be an increase in the bacteria count for a few days, followed by a decrease on the fourteenth

day. This was followed by a more rapid increase until the highest point was reached on the twenty-seventh day. On the thirty-fourth day the counts were about equal to those on the fourteenth day.

Hammer (1912) concludes from his studies with stored ice cream that there is no increase in the number of bacteria during storage, as judged by the number of organisms developing on agar with an incubation temperature of 37° C. He assumes, of course, that the product is kept properly hardened.

Gordon, Prescott, Heinemann, and Pease (1914) noted a marked increase in the bacteria counts of fresh ice cream over the counts of the mix as it entered the freezer.

Esten and Mason (1915) concluded from their investigations that when ice cream is kept frozen for periods of at least a month, there is no marked increase or decrease in the bacteria count as shown by litmus lactose gelatin plate counts.

Ellenberger (1919) noted an increase due to the freezing process, which he thinks may be accounted for by the breaking-up of the clumps of organisms by the beating received from the dasher during freezing. He observed no radical change in the total number of bacteria in ice cream during storage. The groups of bacteria in ice cream as determined by litmus gelatin plates and litmus milk tubes did not change noticeably during storage.

## CAUSE OF DEATH OF THE CELL

Several theories have been suggested to explain the specific action which results in the death of the plant cells when exposed to low temperatures. Du Hamel and Duffon (1737) advanced the theory that death was due to the bursting of the cell wall as a result of the expansion accompanying ice formation. Senebier (cited by Göppert, 1830) also supported this view, which was later disproved by Sachs (1860) and Nägeli (1861). The formation of ice crystals within the cell and in the intercellular spaces was noted by Göppert (1830), but in no case could he find ruptured cells. He considered death a result of freezing, and as being in no way affected by the rate of thaw. Sachs concluded from his results that the degree of killing of plants at a given temperature depended on the rate of thaw.

Müller-Thurgau (1880) and Molisch (1897) were unable to detect any great difference in the amount of killing due to the difference in rate

of thaw, except in a few specific cases. They believed that death was due to the rapid withdrawal of water from the cell to form the ice crystals in the intercellular spaces during the process of freezing, and that only when freezing took place very rapidly were ice crystals formed within the cell. Unfavorable conditions appear in general to reduce the power of resistance to cold, and a deficiency or excess of water or plant food would act in the same way.

Klemm (1895) noted that the visible changes and deformations produced in the protoplasm were due to sudden changes in temperature, and were not present when the cells were subjected to gradual changes.

D'Arsonval (1901) noted that yeasts and bacteria did not lose their vital properties when placed in liquid air for weeks. He thinks the fluid in the cell is probably not solidified if the cell is not ruptured, owing to the enormous osmotic pressure in those small organisms, for if their osmotic tension is lowered by placing them in a solution of sodium chloride, potassium chloride, or glycerin, they are readily killed. He suggests the possibility of determining the osmotic pressure of any given cell by the temperature at which its vitality is destroyed.

Matruchot and Molliard (1901) subjected plants to freezing, to drying, and to the action of solutions of high osmotic concentration. They observed a marked parallelism between the action of freezing and that of drying, and they concur with Molisch in that the death of the cell is due to a rapid drying-out of the tissues.

Mez (1905) noted, in his studies of the effect of supercooling on plant tissue, that where the ice formation began at once on reaching the freezing point the killing was not so great as where there was supercooling, and the formation of ice crystals took place rapidly. He thinks that when a temperature of $-6°$ C. is reached, all solutions will crystallize out. The heat liberated by the crystallizing of the solutions and the formation of ice, will, after the cells are insulated by the ice mass, aid in keeping the temperature of the cell above that of the surrounding material. Mez holds that death is due to the direct effect of the cold.

Gorke (1907) noted that when the cell sap was frozen, certain proteids were precipitated, and that those plants that are most easily killed by freezing have their proteids precipitated at the highest temperatures. By using solutions of albumin to which had been added zinc sulfate, he was able to show that the concentration of the salts had a marked effect

on the precipitation of the proteids when the solutions were frozen. He assumed that killing from cold may be due to the precipitation of the proteids resulting from the concentration of salts in the sap as the water is removed to form the ice crystals within the intercellular spaces.

Heckel (1909) noted that anesthetics and freezing liberated coumarin very rapidly from certain plants, and that the characteristic odor was apparent from green plants in a few moments after freezing, whereas ordinarily it is not apparent until after the plants have become more or less dried. This seemed to indicate that freezing and drying affected the plant in much the same way.

In studying the relation between the density of cell saps and the freezing points of leaves, Ohlweiler (1912) noted that the extreme differences in sap density are generally accompanied by corresponding resistance to freezing. He found that when the cell structure was essentially the same, the density of the cell sap of the species would indicate its relative hardness.

Lepeschkin (1912) concludes that death in plant cells is preceded by a decomposition of the less stable protein compounds and later their coagulation. Capillary forces may play an important part in their coagulation, which in turn sets free energy that leads to the breaking down of the weaker compounds.

Maximow (1914), in his very excellent work in freezing sections of plants in solutions of various strengths of both organic and inorganic substances, found a remarkable protection to be exerted whenever the eutectic point of the substances did not lie too near the freezing point and whenever the substance was not exceedingly toxic. When the sections were immersed in these solutions and immediately frozen, as much protection was noted as when they were permitted to remain in the solution for several hours. The protective action was not in direct proportion to the osmotic pressure and the lowering of the freezing point, for it was considerably more rapid than the latter changes. Since the protective action did not depend on the time the plant was in the solution nor on the permeability of the protoplasm, Maximow concluded that the action is on the outer layer of the protoplasm, and that the withdrawal of water seems to be limited to the plasma membrane.

Chandler (1913) was able to reduce the killing temperature of plant tissue by increasing the sap density of the tissue. In the case of unripe

apples and pears, there was no indication that the rate of thawing had anything to do with the amount of killing at a given temperature.

## SCOPE OF THE PRESENT INVESTIGATION

With the results of the aforesaid workers in mind, the author undertook the investigations herein reported in an attempt to answer the following questions: (1) Is there an actual growth and reproduction of the bacteria in frozen soils or solutions? (2) What is the effect of low temperature on *Bacillus radicicola* in solution, sand, and soil cultures? (3) To what is the protective action noted in solution and soil cultures due? (4) Why have so many investigators obtained such divergent results in their work with bacteria at low temperatures?

The widely varying results obtained by Conn, by Brown and Smith, and by Harder, would seem to indicate that the number of bacteria occurring in frozen soils as determined by the agar-plate method is due not to an actual multiplication of the bacteria but to some unknown condition. The findings of Harder would indicate that the moisture content is of prime importance, whereas Brown and Smith did not consider it so important. Conn found that potted soils showed the same marked increase as the field soils. Harder was unable to show this increase in the potted soils, and concluded that the bacteria were carried up from the lower depths by heavy frosts.

It is contrary to the general conception of plant and animal life to hold that bacteria will grow and multiply more rapidly at temperatures below zero than at the so-called favorable temperatures. The work of Conn, of Brown and Smith, and of Harder, gives little or no evidence to show that the bacteria do actually multiply in frozen soils, for the increase in bacteria counts noted by these investigators was based on the colonies appearing on the agar plates, and, as is well known, this method is in many cases a poor indicator of the actual number of bacteria present. The method is perhaps of value in a comparative way when comparing substances that have received more or less of the same treatment, but it seems very doubtful whether it has any real value when comparing normal and frozen soils. The results obtained by Brown and Smith are very good examples of this.

If there is not an actual increase in the number of bacteria in frozen soils — and it does not seem probable that there is — the large number of

colonies appearing on agar plates must be accounted for in some other way. As each colony on a plate may result from a single cell or from a cluster of many cells, it would seem that the increase obtained from frozen soils might be due to the breaking up of the masses of bacteria, not to an actual reproduction.

Both Conn and Harder considered this breaking-up process to be extremely unlikely, for if such was the case the count immediately after the thaw would not be so nearly the same as it was before the freeze. This objection, however, might not hold in the case of the bacteria, for they often grow in a jelly-like mass which might be ruptured by freezing but which if allowed to thaw gradually, as it would in the soil under a normal condition, might assume its original position. If such was not the case, one might expect more bacteria in recently thawed soil than in unfrozen soil. If the increase was due to a summer and a winter flora, as suggested by Conn, there should not be a rapid decrease in number of bacteria immediately after the thaw, for the soil would maintain for several days a temperature more favorable for the winter than for the summer flora. The soils that were allowed to thaw gradually in the field showed approximately the same number of bacteria as was shown by the soils before they were frozen, whereas the soils that were thawed rapidly in the laboratory showed a higher count. This would seem to indicate that the rate of thaw might be an important factor. The experiments reported herein were conducted with these considerations in mind.

## METHODS OF INVESTIGATION

### ORGANISMS

In the experiments dealing with the field soils, the bacterial flora of the soil was studied as it was observed on examination. A study was made of the different groups, but no marked correlation was noted between certain groups and the treatment of the soil. *Bacillus radicicola* from field pea was used for all the pure-culture work. This organism was selected because of its economical importance and habits of growth. It is easy to grow and identify, and is classed as a non-spore-bearing form. The latter character is of importance in low-temperature studies.

### MEDIA

The organisms were grown in soil, sand, and solution cultures. The medium used for making the plate counts of the field soils was Conn's (1914)

asparaginate agar. The agar used in plating the *Bacillus radicicola* organism was the same as Wilson (1917) used in his studies. In the nutrient solutions the saccharose was replaced by mannite, 1 gram to a liter.

### METHOD OF FREEZING, THAWING, AND PLATING THE BACTERIA

In the case of the field soils, the samples were collected in the field under sterile conditions and 20-gram portions were placed in sterile liter flasks. The samples were then taken to the laboratory in a frozen condition and treated immediately, water at the different temperatures being used to thaw the samples. Plates were poured from the 20,000 and 200,000 dilutions. Five plates were poured from each dilution in all cases. Ice and salt, liquid air, and outside temperatures, were used to freeze the laboratory samples.

The *Bacillus radicicola* organism was grown in sterile sand, soil, and water cultures. In the case of the sand and soil cultures 1-gram portions were weighed out into small, sterile, test tubes under sterile conditions, and subjected to the various treatments. The samples subjected to the liquid-air treatment were lowered into the wide-mouth Dewar bulbs containing the liquid air. Care was necessary to prevent bursting of the tube in freezing. The plates were incubated at 30° C. and counts were made at the end of four and seven days. Five plates from each of three dilutions were poured from all samples.

## EFFECT OF RATE OF THAW ON BACTERIA COUNT

### SOILS FROZEN IN THE FIELD

It would seem that if the large number of bacteria in frozen soils as shown by the plate method is due to the breaking up of the clusters of organisms, the rate of thaw should have some effect. In order to test this point, samples of Dunkirk clay soil containing 33 per cent of moisture were taken from the field in a frozen condition and thoroly mixed, and 20-gram portions were put into liter flasks. These samples were brought to the laboratory and plated by the dilution method. The only difference in the treatment was the temperature of the water blanks used in making the dilutions. The results are shown in table 1.

From the results shown in table 1, the rate of thaw seemed to have a marked effect as shown by the counts on agar plates. The increased count due to the sudden thawing of the soil with water at 30° C. was 200

per cent above that of the count made using water at 1° C. When the soil was allowed to thaw in the air the difference was less marked. It is interesting to note that when the temperature of the water used in plating the soil was raised to 40° C. there was always a drop in the counts. This may have been due to the death of the bacteria caused by the sudden change to higher or lower temperature. It seems more probable, however, that the higher temperatures may cause a greater or less coagulation of the masses, resulting in fewer colonies on the plates.

TABLE 1. EFFECT OF RATE OF THAW ON THE BACTERIA COUNT IN FIELD SOILS

| Sample | Treatment | Bacteria per gram of dry soil |
|---|---|---|
| 1 | Water added at 1° C | 3,100,000 |
| 2 | Water added at 10° C | 5,200,000 |
| 3 | Water added at 20° C | 6,000,000 |
| 4 | Water added at 30° C | 9,300,000 |
| 5 | Water added at 40° C | 6,700,000 |
| 6 | Soil thawed in air at 1° C | 5,000,000 |
| 7 | Soil thawed in air at 10° C | 6,100,000 |
| 8 | Soil thawed in air at 20° C | 6,300,000 |
| 9 | Soil thawed in air at 30° C | 6,900,000 |
| 10 | Soil thawed in air at 40° C | 5,800,000 |

## SOILS FROZEN IN THE LABORATORY

Samples of soil that had been kept in a moist condition in the laboratory were used to test the effect of short periods of freezing and different rates of thaw. Counts were made of the normal soil containing 30 per cent of moisture, and the samples were then exposed to a temperature of −15° C. for twenty-four hours. In table 2 is shown the effect of short periods of freezing and different rates of thaw:

TABLE 2. EFFECT OF RATE OF THAW ON THE BACTERIA COUNT IN LABORATORY SOILS

| Sample | Treatment | Bacteria per gram of dry soil |
|---|---|---|
| 1 | Normal | 4,600,000 |
| 2 | Frozen 2 hours at −16° C., thawed in room | 6,600,000 |
| 3 | Frozen 2 hours at −16° C., water added at 30° C. | 9,800,000 |

There was an increase of about 50 per cent in the bacteria count when the soil was thawed by adding water at 30° C., over the count from the sample allowed to thaw in the air. This would seem to indicate a breaking up of the clusters of bacteria, due to the sudden change in temperature.

## EFFECT OF ALTERNATE FREEZING AND THAWING ON BACTERIA COUNT

If there is a breaking up of the masses of bacteria when subjected to extreme temperatures, then alternate freezing and thawing should have some effect. In the test to determine this point the soil was placed in two containers 10 by 6 by 4 inches in size and divided into compartments by means of strips of paper. One of the containers was brought in each day and allowed to thaw at room temperature, counts were made of the bacteria per gram of soil in one of the compartments, and the container was then placed outside to freeze again. The outer container remained frozen during the experiment. The results are shown in table 3:

TABLE 3. EFFECT OF ALTERNATE FREEZING AND THAWING ON THE BACTERIA COUNT

| Day | Treatment | Bacteria per gram of dry soil |
|---|---|---|
| First | Normal | 4,500,000 |
| Second | Frozen and thawed | 7,000,000 |
| Third | Frozen and thawed | 8,100,000 |
| Fourth | Frozen and thawed | 10,200,000 |
| Fifth | Frozen and thawed | 11,200,000 |
| Sixth | Frozen and thawed | 11,100,000 |
| Seventh | Frozen and thawed | 11,900,000 |
| Eighth | Continually frozen | 8,900,000 |

The results shown in table 3 would seem to indicate that alternate freezing and thawing did have some effect, until the fifth day at least. After that there was little or no increase. There is one thing that must be taken into consideration in all these results, and that is the possibility that some of the bacteria may be killed by freezing and that the number as shown by the plate count may represent a greater breaking-up of the masses than the results would otherwise indicate. Inasmuch as the pots were only 4 inches deep, and the samples from which the counts were made

represented the bottom as well as the top of the soil, the increase could not have been due to the drawing-up of the organisms from the lower depths, as suggested by Harder.

## EFFECT OF TIME, TEMPERATURE, AND RATE OF THAW ON BACTERIA COUNT

### IN CLAY SOILS

The effect of the time of freezing and the rate of thaw on the number of bacteria in frozen soil, and on the bacteria in the dilutions from the soil, is shown in table 4. In the test to determine the latter, samples were taken from the flasks containing the last dilution — the one that was plated out — and were frozen for different lengths of time.

TABLE 4. Effect of Time, Temperature, and Rate of Thaw on the Bacteria Count in Clay Soils

| Sample | Treatment | Bacteria per gram of dry soil |
|---|---|---|
| 1 | Normal soil, water blank at 30° C | 7,500,000 |
| 2 | Normal soil, water blank at 0° C | 6,800,000 |
| 3 | Frozen 2 hours at −15° C., water added at 0° C. | 5,600,000 |
| 4 | Frozen 2 hours at −15° C., water added at 15° C. | 7,100,000 |
| 5 | Frozen 2 hours at −15° C., water added at 25° C. | 8,200,000 |
| 6 | Frozen 2 hours at −15° C., water added at 40° C. | 5,800,000 |
| 7 | Dilution of sample 1, frozen 1 hour | 6,400,000 |
| 8 | Dilution of sample 1, frozen 12 hours | 4,300,000 |
| 9 | Dilution of sample 1, stood 12 hours | 5,700,000 |
| 10 | Frozen in liquid air at −190° C. 1 minute | 8,000,000 |
| 11 | Frozen in liquid air at −190° C. 30 minutes | 7,100,000 |
| 12 | Frozen in liquid air at −190° C. 6 hours | 3,400,000 |

The temperature of the water used in making the dilution seemed to have a marked effect on the bacteria in the frozen soil and a slight effect on the bacteria in the unfrozen soil. These results seem to indicate that the present method of making plate counts should be standardized, and that the temperature of the water blanks used is one of the factors that must be controlled if the results are to be comparable.

When the soil was frozen in liquid air at a temperature of −190° C. for one minute, there was a noticeable increase in the bacteria count which could not be accounted for by actual growth and multiplication.

When the exposure to liquid air was continued for several hours there was a decrease in the number of bacteria.

The effect of freezing seemed to be less harmful on the bacteria in the soil than on those in the soil dilution in the water blanks. When the freezing was continued for 12 hours there was a marked decrease in number of bacteria. It would seem that the more concentrated soil solution acted as a protective agency, and when the solution was weakened the effect of low temperatures was more marked.

### IN SANDY SOILS

The soil used by Harder in his work was a rich sandy loam, and as his results were so marked it was thought advisable to compare a sandy loam soil with the Dunkirk clay soil. The results obtained when a light sandy soil was used are shown in table 5:

TABLE 5. EFFECT OF TIME, TEMPERATURE, AND RATE OF THAW ON BACTERIA COUNT IN SANDY SOIL

| Sample | Treatment | Bacteria per gram of dry soil |
|---|---|---|
| 1 | Normal soil, water blank at 24° C | 6,400,000 |
| 2 | Frozen in liquid air 5 minutes, thawed at 1° C | 4,800,000 |
| 3 | Frozen in liquid air 5 minutes, thawed at 10° C | 5,400,000 |
| 4 | Frozen in liquid air 5 minutes, thawed at 24° C | 6,800,000 |
| 5 | Frozen in liquid air 5 minutes, thawed at 30° C | 5,600,000 |
| 6 | Frozen in liquid air 5 minutes, thawed at 38° C | 4,800,000 |
| 7 | Frozen in liquid air 1 minute, thawed at 24° C | 5,400,000 |
| 8 | Frozen in ice and salt 1 minute, thawed at 24° C | 7,200,000 |
| 9 | Frozen in ice and salt 2 hours, thawed at 24° C | 14,000,000 |
| 10 | Frozen in liquid air 2 hours, thawed at 24° C | 11,600,000 |

There was the same increase in the bacteria count due to the rate of thaw as noted in the earlier work, and a drop in the bacteria count when the temperature of the water blanks was raised to 30° C. and above. When the soil was frozen in ice and salt for one minute, there was an increase of nearly one million bacteria per gram of soil over the count for the normal soil. When the soil was frozen for two hours in ice and salt, the count increased to 14,000,000, showing an increase of 120 per cent over the count for the normal soil. When the soil was frozen in liquid air for two hours there was also a marked increase. It is evident that this

increase could not have been due to growth and reproduction of the bacteria in the unfrozen soil solution, as suggested by Brown, but that it must have been due to the breaking up of the clumps of bacteria.

The results from the liquid-air treatment would indicate that there is a breaking up of the clusters of bacteria sufficient to show a marked increase above the number in normal soil. When it is considered that probably many of the bacteria were killed by the low temperature, it seems evident that the breaking-up process must be even greater than the plate counts indicate.

## AMMONIFICATION AND NITRIFICATION IN FROZEN SOILS

In order to test the bacterial activities in frozen soils more carefully, the ammonifying and nitrifying powers of frozen soils were studied. Peptone and casein were added to the soils at the rate of $\frac{1}{2}$ gram to 100 grams of soil. The determinations of ammonia were made at the beginning of the experiment and at the end of five days. One-half of the samples were placed in the incubator at 22° C., and the other half were kept frozen during the experiment. The determinations of nitrates were made at the beginning of the experiment and at the end of four weeks. The samples were treated the same as in the ammonification experiment. The results are shown in table 6:

TABLE 6. Ammonification and Nitrification in Frozen and in Unfrozen Soils

| Treatment | Parts per million of dry soil | | | |
|---|---|---|---|---|
| | Ammonia nitrogen | | Nitrate nitrogen | |
| | At beginning of experiment | At the end of 5 days | At beginning of experiment | At the end of 4 weeks |
| Soil and peptone, frozen | 65.4 | 68.7 | 112 | 118 |
| Soil and peptone, incubated | 65.4 | 382.9 | 112 | 253 |
| Soil and casein, frozen | 56.1 | 55.3 | 112 | 116 |
| Soil and casein, incubated | 56.1 | 336.9 | 112 | 237 |

These results show that there is little or no change going on in the soil solution when it is in a frozen state. This indicates that no protoplasmic activity, such as growth or reproduction, is taking place.

## EFFECT OF LOW TEMPERATURE ON BACILLUS RADICICOLA

Since little or no work has been done in studying the effect of low temperature on pure cultures of the soil bacteria, it was deemed advisable to use the non-spore-bearing organism *Bacillus radicicola*, because of its economic importance. Since this is the organism used for inoculating the legume plants, it was thought that if low temperature does have a marked effect on its development, this fact might throw some light on the soil-inoculation question.

The method employed was to grow the bacteria in pure cultures in nutrient solutions, sand, and soil, and then subject them to different degrees of temperature for varying lengths of time. The nutrient solution used was the one recommended by Wilson (1917) in his studies of *Bacillus radicicola*. The saccharose in the original solution was replaced by mannite, using 1 gram per liter. The larger amount of sugar tended to increase the viscosity of the growth, which rendered it less favorable for quantitative work. The soil used was of the Dunkirk series. Counts were made by the agar-plate method. The medium used was the same as the nutrient solution mentioned above, with the addition of 1.5 per cent agar. The 10 grams of soil — or, in the case of the nutrient solution, 1 cubic centimeter — was added to water blanks until the desired dilution was obtained. Five plates were poured from each dilution, and three dilutions were used in all cases for pouring the plates. Separate counts were made in all cases and the averages of the five plates were taken for the final counts. The results in table 7 represent the findings on 1350 plates.

All freezing was done in thin-walled glass tubes. In the solution tests the bacteria were grown in the test tubes in which they were later frozen. Five-hundred-gram portions of the sterile soil and sand were inoculated with the bacteria and maintained for one week at 25° C. Tests were made of these samples by weighing out one-gram portions into sterile tubes and subjecting them to the low temperatures. The samples were then added to 500-cubic-centimeter water blanks, in a frozen condition. An attempt was made to keep uniform all conditions that were not being studied. By lowering the tubes gradually into the liquid air it was possible to freeze them without breaking the glass.

In interpreting the results shown in table 7, the fact must be kept in mind that the present method of determining the number of bacteria is very

unsatisfactory, especially when working with frozen soils. The colonies on the plate may represent a single cell or a mass of cells, and, altho the number of colonies may be greater after freezing, the investigator is not at all sure that a great many of the organisms have not been killed and that the seeming increase is due to the breaking up of the clusters.

TABLE 7. INFLUENCE OF LOW TEMPERATURE ON BACILLUS RADICICOLA IN SOLUTION, SAND, AND SOIL CULTURES

| Sample | Treatment | Bacteria per cc. of solution | Bacteria per gram | |
|---|---|---|---|---|
| | | | Sand | Soil |
| 1 | Normal soil | 3,000,000 | 3,700,000 | 400,000,000 |
| 2 | Frozen with ice and salt at -15° C. 3 minutes | 1,400,000 | 5,200,000 | 470,000,000 |
| 3 | Frozen with ice and salt at -15° C. 1 hour | 1,000,000 | 3,200,000 | 500,000,000 |
| 4 | Frozen with ice and salt at -15° C. 2½ hours | 750,000 | 3,000,000 | 520,000,000 |
| 5 | Frozen with ice and salt at -15° C. 6 hours | 600,000 | 2,800,000 | 400,000,000 |
| 6 | Frozen in liquid air at -190° C. instantaneously | 1,000,000 | 2,700,000 | 470,000,000 |
| 7 | Frozen in liquid air at -190° C. 30 minutes | 750,000 | 2,200,000 | 380,000,000 |
| 8 | Frozen in liquid air at -190° C. 1 hour | 620,000 | 2,100,000 | 360,000,000 |
| 9 | Frozen in liquid air at -190° C. 2½ hours | 600,000 | 2,600,000 | 530,000,000 |
| 10 | Frozen in liquid air at -190° C. 6 hours | 450,000 | 2,100,000 | 400,000,000 |

In table 7 it is shown that there is a gradual decrease in the number of bacteria in the solution as the degree of cold and the time of freezing is continued. In the sand cultures there was a marked increase in the number of bacteria when frozen for a few minutes at -15° C. This would indicate a breaking up of the clusters of bacteria that may surround the sand particles. A slight protective action was present in the sand and soil cultures that was not noticed in the solution cultures. The length of time of freezing had very little effect when liquid air was used. In sand the total count was slightly below normal, and remained so during the test.

The results obtained with the soil cultures are interesting and give some idea of what may be expected in such work dealing with the bacterial

flora of the soil. The results show no difference between the total counts of the normal soil and those of the samples that had been exposed to the temperature of liquid air for six hours, or those frozen with ice and salt for six hours. The samples exposed to the temperatures of −15° and −190° C. both showed a marked increase over that of the normal soil, again indicating a breaking-up process. It would seem that the non-spore-bearing bacteria, such as *Bacillus radicicola*, are able to withstand the effect of low temperature of the soil. Careful work on the bacterial-activity problem would doubtless verify this supposition. All evidence points to the probability that the effect of freezing on the soil is physical, not bacteriological.

## INFLUENCE OF CONCENTRATION OF THE MEDIUM ON THE DEATH OF BACTERIA AT LOW TEMPERATURES

The results obtained with *Bacillus radicicola* in solution and soil cultures would seem to indicate that the concentration of the solution surrounding the bacteria had something to do with the ability of the bacteria to withstand low temperatures. The work of Maximow (1914) showed that such a protective action was evident when plants were placed in solutions of high concentrations. This protective action noted in the soil may have been due to the concentration of the soil solution or to some other factor such as the influence of surface tension on the large and the small soil particles.

If the death of the bacterial cell when frozen is due to the withdrawal of water from the semi-permeable membrane, or outer layer of the cell, resulting in the precipitation of the proteids, then it should be possible to overcome this harmful effect of freezing by increasing the concentration of the cell sap. The greater the concentration of the cell sap within the cell, the greater would be the osmotic pressure, the greater the power of inhibition, and the greater the resistance of the cell to low temperatures.

There is a possibility that the surface tension may be so great on the small particles that it would prevent the freezing of the solution. But when one considers that a pressure of 2600 atmospheres is necessary to prevent starch grains from absorbing water, and a pressure of 13,000 atmospheres is necessary to prevent water from freezing at −20° C., one realizes that if the surface tension does play an important part in the soil solution the pressure must be very great.

### INFLUENCE OF GLYCERIN

If the protective action is due to the greater concentration of the solution, the addition of sugar or similar substances should have the same effect. In order to test the influence of the concentration of the medium, a very weak nutrient solution was prepared as follows: Dibasic potassium phosphate 0.05 gram, magnesium sulfate 0.05 gram, sodium chloride 0.05 gram, calcium sulfate 0.05 gram, distilled water 1000 cubic centimeters. Glycerin was added at the following rates: 0.01, 0.05, 0.1, 0.5, 1, 5, 10, and 15 per cent.

Test tubes containing 10 cubic centimeters of the above nutrient solution with glycerin added in increasing amounts, were inoculated with a culture of *Bacillus radicicola* and incubated for five days at 25° C. At the end of that period, counts were made of the number of bacteria per cubic centimeter in each tube, by means of the agar plates. The tubes were then frozen for thirty minutes in ice and salt at a temperature of −15° C. At the end of the half hour the tubes were thawed by placing them in water at 15° C., and were plated as in the preceding experiments. Care was taken to have all conditions uniform, for the earlier findings indicate that a difference in the temperature of the water blanks or in the rate of thaw might make a difference in these results. All counts were made at the end of five days incubation. Nine plates were poured from each tube and the experiment was run in triplicate, so that each count represents the average of twenty-seven plates.

TABLE 8. INFLUENCE OF GLYCERIN ON THE DEATH OF BACTERIA WHEN FROZEN AT −15° C.

| Sample | Glycerin (per cent) | Normal bacteria count | Bacteria count after being frozen for 15 minutes | Per cent of bacteria killed |
|---|---|---|---|---|
| 1 | None | 5,600,000 | 236,000 | 96 |
| 2 | 0.01 | 12,300,000 | 984,000 | 92 |
| 3 | 0.05 | 13,600,000 | 1,768,000 | 87 |
| 4 | 0.1 | 17,000,000 | 10,000,000 | 41 |
| 5 | 0.5 | 21,000,000 | 11,550,000 | 45 |
| 6 | 1.0 | 23,000,000 | 23,100,000 | 0 |
| 7 | 5.0 | 24,300,000 | 28,200,000 | 0 |
| 8 | 10.0 | 520,000 | 546,000 | 0 |
| 9 | 15.0 | No growth | No growth | ..... |

The results obtained when glycerin was used in varying amounts are shown in table 8. A remarkable protective action was exerted by the glycerin when the concentration was 1 per cent and above. With decreasing amounts of glycerin down to 0.01 per cent, there was a rapid increase in the percentage of bacteria killed. When the concentration of glycerin was raised to 5 and 10 per cent, there was an actual increase in the number of bacteria, as is shown by the colonies on the agar plates. This seeming increase was perhaps due to the breaking up of the clumps of bacteria. It is possible that in the nutrient solution containing 1 per cent of glycerin a great many of the organisms were killed, and that the high counts were due to the breaking up of the masses of bacteria. There was little or no growth in the nutrient solutions containing 15 per cent of glycerin.

### INFLUENCE OF DEXTROSE

The results from the higher concentrations of media using glycerin and dextrose verified the finding of Maximow in his work with red cabbage and *Tradescantia discolor*. So long as the temperature of the frozen medium was maintained above the eutectic point of the substance used, the protective action was noted. If the above findings hold true in regard to the bacterial cell, the concentration of the medium should have no effect when the temperature is lowered to a point at which the glycerin and the dextrose will crystallize out. To test this latter point, the bacteria in the solutions described above were subjected to a temperature of −190° C., using ice and salt.

The results obtained with the different concentrations of media when exposed to a temperature of −190° C. using liquid air, and to a temperature of −15° C. using ice and salt, are given in table 9. There was the same marked protective action due to the increased concentration of the medium when the solutions were frozen in ice and salt for two hours, as was shown by glycerin (table 8). When the bacteria were subjected to the temperature of liquid air for five minutes the concentration of the medium had little or no effect. These results would seem to substantiate the foregoing theory, that when the temperature is lowered below that of the eutectic point of the sugars added, the concentration of the medium has no effect.

In table 9 the percentage of bacteria killed is based on the number of colonies growing on the plates poured before and after treatment of the

samples. The normal is considered as 100 per cent and the decrease is given as per cent killed. It is interesting to note that the concentration of the medium had no effect when the temperature was lowered below the eutectic point of the sugar, but at temperatures about the eutectic point the sugar showed a marked protective action.

TABLE 9. Influence of Dextrose on the Resistance of Bacteria to Low Temperatures

| Sample | Dextrose (per cent) | Normal bacteria count | Bacteria count when frozen in liquid air for 5 minutes | Per cent of bacteria killed | Bacteria count when frozen in ice and salt for 2 hours | Per cent of bacteria killed |
|---|---|---|---|---|---|---|
| 1 | None | No growth | ..... | ..... | ..... | ..... |
| 2 | 0.01 | 880,000 | 570,000 | 35 | 17,600 | 98 |
| 3 | 0.05 | 1,960,000 | 1,240,000 | 37 | 98,000 | 95 |
| 4 | 0.1 | 3,600,000 | 2,400,000 | 33 | 398,000 | 89 |
| 5 | 0.5 | 4,700,000 | 2,490,000 | 47 | 1,220,000 | 74 |
| 6 | 1.0 | 16,400,000 | 9,480,000 | 42 | 6,890,000 | 58 |
| 7 | 5.0 | 24,100,000 | 16,390,000 | 32 | 15,660,000 | 35 |
| 8 | 10.0 | 11,300,000 | 8,140,000 | 28 | 10,850,000 | 4 |
| 9 | 15.0 | 8,200,000 | 4,670,000 | 43 | 8,000,000 | 2 |

## GENERAL DISCUSSION

It is evident from the data given that the so-called increase in the number of bacteria in frozen soils is due, not to an actual multiplication and growth of the bacteria in the soil solution as suggested by Conn, but rather to a breaking up of the clumps of bacteria which results in an increased number of colonies on the agar plates. This view is substantiated by the fact that the same increase and decrease in counts may be obtained in the laboratory by freezing the soil for a few minutes and then thawing it out by means of water blanks at different temperatures.

The fact that the same marked increase may take place in soils when frozen in liquid air at a temperature of −190° C. for a few hours, invalidates Brown's theory that the increased growth takes place in the uncongealed hygroscopic water of the soil, for at this low temperature the amount of water remaining uncongealed could hardly be considered sufficient for the favorable growth of bacteria.

It is interesting to note that Conn's counts for the frozen soil were higher than those for the unfrozen soil, whereas the counts of Brown and Smith for the frozen soil were in all cases except one far below those for the unfrozen soil, and in the sample taken on March 1, in which the count was above normal, the moisture content had been increased from 15.76 to 26.57 per cent. Regardless of the fact that three samples out of the four taken showed a lower bacteria count than the normal soil, Brown and Smith concluded that their results substantiated the conclusion of Conn that bacteria do reproduce in increasing numbers in frozen soil.

It is interesting to note the very close correlation that can be drawn between the increase in the number of bacteria in frozen soils and the increase in the individual over the group counts, as shown by Conn in recent publications (1917 and 1918). In both cases the increase was between 25 and 50 per cent, the individual count showing the greater gains. The gains obtained by the author with the frozen samples are in very close keeping with the preceding.

The moisture content and the rate of thaw are the important factors that determine to a large extent the breaking-up process. This point is well brought out in the work of Harder. When the frozen soil was thawed rapidly by rain there were a large number of organisms occurring in the thawed soil, but when the thaw was gradual the number dropped back to about normal. The only high count obtained by Brown and Smith can be explained in somewhat the same manner. Their sample taken on February 11 showed a moisture content of 15.7 per cent and a bacteria count of 4,744,000 colonies; whereas their sample taken on March 1 showed a moisture content of 26.5 per cent and a bacteria count of 16,870,000. Between these two dates the moisture content rose 68 per cent, which would indicate that there had been a thaw followed by a freeze, resulting in a breaking up of the masses of bacteria.

That frozen soil is not as favorable a medium as unfrozen soil for the growth of bacteria is shown by the results obtained by Harder when soils were treated with dextrose. His results show a retardation in growth caused by low temperature, which even a much higher moisture content was not sufficient to counteract. They substantiate the theory that the increased count in frozen soils is due to a breaking up of the clumps of bacteria, for such an increase should be more marked in soils having a high moisture content and this condition was found to be true

in almost all cases. When the soil was thawed rapidly by rain, the count in the thawed soil was very much higher than when the thaw was gradual, indicating a breaking-up process due to the rapid thaw. When the conditions for an actual increase and growth were brought about by the addition of dextrose to the soil, the unfrozen sample showed a much greater increase in bacteria content than did the frozen sample. All this would seem to prove that frozen soil is not as favorable a medium as unfrozen soil for the growth of bacteria. That the increase is not due to mechanical transportation by moisture coming up from below during heavy frosts was shown by Conn in his work with potted soils, and also in the results herein reported, in which the same marked increase was obtained when small amounts of the soil were frozen in test tubes and an entire portion was used in making the dilutions.

The conclusions of Brown and Smith in regard to bacterial activities in frozen soils have not sufficient evidence to give them weight. It is interesting to note how their idea of a summer and a winter flora has been made to fit in with their results. Altho they concluded that the ammonifying power of the frozen soil is increased, the smallest amount of ammonia was produced from the sample taken during the coldest period of the tests. When it is considered that Brown and Smith used a soil infusion representing 5 grams of the frozen soil to inoculate 100 grams of air-dry soil, the results are not surprising. It would seem that the experiment under such conditions could better be called a study of the effect of storing air-dry soil on the bacterial flora therein, inasmuch as the number of bacteria present in the air-dry soil was several times that in the 5 grams of frozen soil. Duplicate tests might perhaps have eliminated the marked variations obtained by Brown and Smith. The tests that should have shown the difference, if there really was one, were those on nitrification, for the condition surrounding those tests are more easily controlled, and the measured product, nitrates, is not so easily lost as are some of the other products. The nitrification results of Brown and Smith indicated that if there was a difference their method was not sufficiently accurate to show it. It would seem that a similar conclusion may be applied to all their results.

Brown and Smith concluded from their nitrification results that the nitrifying power of the soil was rather weak. This is contrary to the findings of Lyon and Bizzell, who noted a beneficial effect due to freezing.

If there was active growth and reproduction of the ammonifying and other types of organisms in the soil, one would expect a protoplasmic activity that would be indicated quantitatively or qualitatively by the formation of ammonia and similar products. As no change was noticeable in the frozen soil, even when large amounts of nitrogenous materials were added, it would seem as if bacterial activities had ceased.

If the bacterial flora of the soil can withstand the low temperature of liquid air for several hours, it seems probable that the mild temperatures to which our soils are subjected during the winter would have little or no effect in changing the bacterial flora therein, and it will require more careful work than has yet been done on the bacterial activities in frozen soils to prove that such a change does take place.

The results obtained by investigators in the field of soil colloids seem to indicate a physical change in the soil due to freezing. It is probably this physical change in the soil and its colloids that influences the bacterial activities, rather than a change in the bacterial flora of the soil.

There is a possibility that pressure may play some part in cell division, for the soil is subjected to considerable pressure during the formation of ice from the soil solution. Kny (1896) noted that pressure actually induced cell division in the pith of Impatiens, and that very pronounced pressure will cause the periclinal divisions of the cambium to cease and anticlinal ones to appear. In many cases he found that pressure induced he formation of cell walls at right angles to its line of action. The close correlation between the high moisture content and the large number of bacteria occurring in the frozen soil seems to favor this theory, for the greater the moisture content, the greater would be the pressure. The fact that small quantities of soil placed loosely in test tubes and frozen showed the same increase, would, however, seem to indicate that the increase was not due to pressure.

The wide variations found by many careful investigators in their studies of the influence of low temperatures on bacteria, may be accounted for by the difference in the concentration of the media in which the bacteria were grown. The fact that 98 per cent of the organisms growing in a very rich nutrient solution survived the low temperature, would seem to support the theory that the higher the concentration of the medium surrounding the cell, the higher will be the concentration of the

cell sap within the cell, which in turn enables the cell to resist freezing at temperatures sufficiently low to freeze the cells containing a weaker solution.

## SUMMARY

The increase in the bacteria counts of frozen soils, as determined by the agar-plate method, is due to the breaking up of the clumps of bacteria, not to growth and multiplication.

There seems to be no change in the bacterial flora of the soil due to freezing. The bacterial activities are influenced only in so far as the physical properties of the soil are affected.

The concentration of the medium, the length of time of the exposure, and the degree of cold, are the three important factors that determine the power of resistance of the bacteria to low temperature.

The protective action due to the concentration of the medium seems to be effective only in cases in which the eutectic point of the substances in solution is below the temperature of the exposure. When the bacteria were exposed to the temperature of liquid air the concentration of the medium had less effect.

The death of the bacterial cell when exposed to low temperature seems to be due to the withdrawal of water from the semi-permeable membrane, or outer layer of the cell.

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# FEED CONSUMED IN MILK PRODUCTION

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# FEED CONSUMED IN MILK PRODUCTION

H. A. Hopper, H. M. Bowen, and F. S. Barlow [1]

To maintain a dairy herd on a satisfactory plane of production necessitates the use of large quantities of concentrated feeding stuffs. In the past, New York dairymen have obtained their supply of this material from distant sources, and it represents a large proportion of the cost of producing milk. For years the tendency among these producers has been to use their lands largely to supply roughage, such as hay, fodder, and silage, and for grazing purposes, looking elsewhere for the concentrates necessary to balance the ration. When such supplementary feeding stuffs were cheap and plentiful they were used as occasion demanded, with small regard to their relative feeding values or to the profit or loss on the enterprise. During more recent years the rapid advance in the cost of supplies has similarly affected feeding stuffs, with the result that the purchase cost of feeds desired by a dairyman is often disproportionate to the selling price of his product. The selection and use of feeds and their relation to profitable production are therefore subjects of very great importance.

## DATA AVAILABLE

Dairying is obviously the leading agricultural industry of New York State, and many agencies are here at work studying the business of milk production. The extension of the practice of testing cows for individual records of performance, thru cow-testing associations and similar agencies under the direction of the farm bureau managers, has made available a considerable amount of information on feed costs and production which should be recognized as a valuable contribution to an economic study of the subject. As this work develops and becomes more carefully supervised, its value will become more generally recognized.

The data forming the basis of discussion in this study were obtained from carefully supervised cow-testing-association records made in Wyoming and Otsego Counties during the years 1914 and 1915. There follows herewith a discussion of the summarized data on the feeding and production records of 847 cows in such associations. Many more records than these were taken and studied, but only those which were complete as to production and feeding for the year are reported here.

[1] H. A. Hopper is Professor of Animal Husbandry at the New York State College of Agriculture, Cornell University. H. M. Bowen and F. S. Barlow are the county agents, respectively, of the Wyoming County Farm Bureau and the Otsego County Farm Bureau.

The record book in use by the cow-testing associations in this State report, in addition to production, only the cost of roughage and grain. It seemed desirable also to determine the kinds and quantity of feed consumed by each cow in making her record. For this purpose supplementary record blanks were furnished the testers by the Department of Animal Husbandry at the New York State College of Agriculture, for reporting these data monthly in detail. Further, each farm was visited by a member of the Department of Animal Husbandry for the purpose of making a survey of the milk production enterprise and to check the testing association report. This summarized report represents, therefore, the cooperative efforts of the Department of Animal Husbandry of the College of Agriculture,[2] the Wyoming County Farm Bureau, and the Otsego County Farm Bureau.

### NUTRIENT BASIS OF COMPARISON DESIRABLE

Production of milk and butterfat, other things being favorable, is dependent on the digestible nutrients supplied to the cow. Prices for feed and supplies may vary from year to year, but digestible nutrients or their equivalent must remain uniform. Feed represents such a large proportion of the cost of production that it has seemed worthy of emphasis in this discussion rather than a report of the results in terms of actual cost. Such a basis will doubtless prove most useful, as it affords a common ground of comparison regardless of prevailing economic conditions.

### FEED UNIT USED

The feed unit employed in this bulletin is one pound of total digestible nutrients. This measure was selected, not for its scientific accuracy, but for its practical value. Present teaching and practice in the formulating of rations is based on digestible nutrients. The feeding standards in common use indicate the nutritive requirements of the various animals in terms of total digestible nutrients. This is the common basis of comparison in use.

To some extent it is true that the digestion coefficients of the various feeding stuffs are likely to vary widely, and that digestible nutrients may not be a true measure of the real value of feeds. The use of the therm, or the energy value of feeds, has been suggested as more nearly accurate. However, since for many of the feeds these values are not known, to compute them would be no more nearly accurate than to use their digestible nutrients. This is especially true of the proprietary feeds. Some

[2] Professors C. H. Royce and C. A. Boutelle, of this College, made the farm surveys, checked the books, and assisted in the final summarizing of the figures.

careful comparisons have shown the digestible nutrients to be practically the same as the therms. To avoid confusion, therefore, it has seemed advisable to use in this bulletin one pound of total digestible nutrients as the feed unit of comparison.

### *Unit — how computed*

In determining the digestible nutrients consumed by each cow, care was exercised to compute from the monthly feed reports the exact quantity and kinds of roughage and grain supplied to her. Each kind of roughage, succulent or dry, was listed separately. The various mixtures of concentrate by-products were split into their several parts and listed accordingly. For the straight roughages and standard by-products, the digestible protein and total digestible nutrients were computed according to Henry and Morrison for the quantity of each feed used. The sum of the number of pounds of total digestible nutrients derived from the various feeds allowed, represents the total number of pounds of total digestible nutrients consumed by the cow.

The total digestible nutrients supplied by a given ration, or group of feeds, is computed as follows: Let it be assumed that the ration consumed by a certain cow contained, according to the standard table of composition of feeding stuffs, the following proportion of digestible nutrients:

| | Total digestible nutrients |
|---|---|
| Protein 2.7 pounds | 2.7 |
| Carbohydrates 14.5 pounds | 14.5 |
| Fats 1.1 pounds × $2\frac{1}{4}$ | 2.475 |
| | 19.675 |

The above ration thus contains 19.675 pounds of total digestible nutrients. To the digestible protein and the digestible carbohydrates should be added the digestible fat multiplied by $2\frac{1}{4}$. The result is pounds of total digestible nutrients, or the feed unit of comparison to be used.

Some proprietary or ready-mixed feeds were used, the formulae for the preparation of which are not known. In order to compute their content of total digestible nutrients, use was made of the New York State Agricultural Experiment Station reports of their analysis as to crude protein, crude fiber, and crude fat. To supplement these a coefficient of digestibility was used to correspond to the ingredient found to be present in largest proportion in the respective feeds. In most cases the proportion of such feeds was not large.

The conclusion to report in terms of digestible nutrients the results obtained from this study does not imply the superiority of this over any

other method. The plan here adopted has seemed the most practicable and effective for the purposes of this discussion.

*Pasture not included*

There seems to be no satisfactory way to measure the nutritive value of pasture to the animal. The number of days on pasture may be reported, but this affords no information as to the quality of the food offered or the quantity consumed by the animal. For these and other sufficient reasons, the pounds of total digestible nutrients reported in this discussion are those consumed exclusive of pasture.

## FEED CONSUMED BY INDIVIDUALS WHERE COMPLETE RECORDS WERE KEPT

For the specific information offered, and to serve as a check on the records from cow-testing associations to be considered later, it has seemed desirable to set forth the feed records of individual cows where it was possible to obtain the carefully weighed amounts of food consumed by each in a year. The itemized feed records of three cows have been selected and appear in tables 1, 2, and 3. The production per cow ranges from 5497 to 13,710 pounds of milk. The digestible nutrients consumed per cow range from 2492 to 7537 pounds. These tables indicate the kinds and the quantities of food required for the production indicated in each case. They are of the greatest value in showing the individual requirements for food in order to attain a given production.

TABLE 1. FOOD CONSUMED BY A GRADE HOLSTEIN COW PRODUCING 5497 POUNDS OF MILK, 196 POUNDS OF BUTTERFAT

| | Quantity (pounds) | Total digestible nutrients |
|---|---|---|
| Mixed hay | 1,480 | 684 |
| Corn silage | 4,250 | 752 |
| Corn fodder, dry | 1,180 | 634 |
| Ground oats | 84 | 59 |
| Ground barley | 84 | 67 |
| Gluten feed | 116 | 94 |
| Four X distillers' grains | 169 | 150 |
| Wheat bran | 85 | 52 |
| Total | ..... | 2,492 |

| | |
|---|---|
| Succulent feed (pounds) | 4,250 |
| Dry roughage (pounds) | 2,660 |
| Grain (pounds) | 538 |

TABLE 2. FOOD CONSUMED BY A GRADE HOLSTEIN COW PRODUCING 10,450 POUNDS OF MILK, 348 POUNDS OF BUTTERFAT

| | Quantity (pounds) | Total digestible nutrients |
|---|---|---|
| Corn silage | 10,293 | 1,822 |
| Green oats | 1,860 | 296 |
| Green alfalfa | 150 | 22 |
| Corn fodder, dry | 1,525 | 819 |
| Mixed hay | 2,486 | 1,149 |
| Grandin Stock Food | 503 | 277 |
| Cottonseed meal | 700 | 547 |
| Bran | 634 | 386 |
| Oil meal | 194 | 151 |
| Faramel Dairy Ration | 826 | 479 |
| Oats | 53 | 37 |
| Total | ..... | 5,985 |

| | |
|---|---|
| Succulent feed (pounds) | 12,303 |
| Dry roughage (pounds) | 4,011 |
| Grain (pounds) | 2,910 |

TABLE 3. FOOD CONSUMED BY RENA ROSS 3d PRODUCING 13,710 POUNDS OF MILK, 551.8 POUNDS OF BUTTERFAT

| | Quantity (pounds) | Total digestible nutrients |
|---|---|---|
| Corn silage | 8,000 | 1,416 |
| Mixed hay | 2,400 | 1,108 |
| Green corn | 4,500 | 630 |
| Beets | 1,200 | 122 |
| Corn meal | 300 | 257 |
| Wheat bran | 1,460 | 889 |
| Distillers' dried grains | 1,460 | 1,297 |
| Alfalfa meal | 730 | 370 |
| Gluten meal | 912 | 766 |
| Cottonseed meal | 912 | 682 |
| Total | ..... | 7,537 |

| | |
|---|---|
| Succulent feed (pounds) | 13,700 |
| Dry roughage (pounds) | 2,400 |
| Grain (pounds) | 5,774 |

## RELATION OF PRODUCTION TO FEED CONSUMED OTHER THAN PASTURE

A significant measure of individual efficiency is the ability of a cow to produce from a definite amount of feed. Since a consideration of each individual in this respect is not feasible, grouping them according to production serves the same end. In tables 4, 5, 6, and 7, the feed and production records of 847 cows for one year, in three cow-testing asso-

ciations in Wyoming and Otsego Counties, are arranged for comparison according to the amount of milk produced. The groups used and the data on each are presented as follows: for cows having a production below 5000 pounds, in table 4; for production from 5000 to 7000 pounds, in table 5; for production from 7001 to 9000 pounds, in table 6; for production above 9000 pounds, in table 7.

The lowest-performance group (table 4) includes 335 records below 5000 pounds, or 39.6 per cent of the cows reported. The next higher group, from 5000 to 7000 pounds, includes 368 records, or 43.4 per cent of the cows. The next higher group, from 7001 to 9000 pounds, includes 112 records, or 13.2 per cent of the cows. The last, or highest, group, with a production above 9000 pounds, includes 32 records, or 3.8 per cent of the cows. In tables 4 to 7 the essential facts concerning these records are shown in their respective groups.

TABLE 4. RECORDS FOR COWS PRODUCING LESS THAN 5000 POUNDS OF MILK A YEAR

| | Wethersfield | Otsego | Perry Pike | Average |
|---|---|---|---|---|
| Number of cows, 335, or 39.6 per cent | 137 | 73 | 125 | ..... |
| Milk produced (pounds) | 3,988.2 | 3,931.3 | 3,857.2 | 3,925.6 |
| Butterfat produced (pounds) | 160.7 | 188.9 | 166.1 | 171.9 |
| Succulent roughage consumed (pounds) | 3,356.2 | 4,499.0 | 3,745.6 | 3,866.9 |
| Dry roughage consumed (pounds) | 2,405.2 | 1,456.8 | 3,234.5 | 2,365.5 |
| Grain consumed (pounds) | 874.2 | 1,240.3 | 724.5 | 946.3 |
| Total digestible nutrients (pounds) | 2,246.7 | 2,033.1 | 2,610.5 | 2,296.8 |
| Total digestible nutrients to 1 pound of butterfat (pounds) | 14.0 | 10.8 | 15.7 | 13.4 |
| Total digestible nutrients to 100 pounds of milk (pounds) | 56.3 | 51.7 | 67.7 | 58.5 |

Ratio of grain consumed to milk produced, 1:4.1.

TABLE 5. RECORDS FOR COWS PRODUCING FROM 5000 TO 7000 POUNDS OF MILK A YEAR

| | Wethersfield | Otsego | Perry Pike | Average |
|---|---|---|---|---|
| Number of cows, 368, or 43.4 per cent | 161 | 68 | 139 | ..... |
| Milk produced (pounds) | 5,959.9 | 6,035.6 | 5,952.8 | 5,982.8 |
| Butterfat produced (pounds) | 230.2 | 245.9 | 262.0 | 246.0 |
| Succulent roughage consumed (pounds) | 3,661.0 | 5,244.5 | 5,198.3 | 4,701.3 |
| Dry roughage consumed (pounds) | 2,413.9 | 1,580.5 | 2,791.3 | 2,261.9 |
| Grain consumed (pounds) | 1,092.6 | 1,828.1 | 1,190.0 | 1,370.2 |
| Total digestible nutrients (pounds) | 2,584.7 | 2,747.2 | 3,131.4 | 2,821.1 |
| Total digestible nutrients to 1 pound of butterfat (pounds) | 11.2 | 11.2 | 11.9 | 11.5 |
| Total digestible nutrients to 100 pounds of milk (pounds) | 43.4 | 45.5 | 52.6 | 47.1 |

Ratio of grain consumed to milk produced, 1:4.4.

TABLE 6. RECORDS FOR COWS PRODUCING FROM 7001 TO 9000 POUNDS OF MILK A YEAR

| | Wethersfield | Otsego | Perry Pike | Average |
|---|---|---|---|---|
| Number of cows, 112, or 13.2 per cent | 51 | 29 | 32 | ..... |
| Milk produced (pounds) | 7,783.2 | 7,762.7 | 7,669.3 | 7,708.4 |
| Butterfat produced (pounds) | 279.5 | 291.2 | 293.0 | 287.9 |
| Succulent roughage consumed (pounds) | 4,303.6 | 6,168.4 | 7,135.8 | 5,869.3 |
| Dry roughage consumed (pounds) | 2,447.0 | 1,698.0 | 2,651.7 | 2,265.6 |
| Grain consumed (pounds) | 1,406.9 | 2,147.0 | 1,446.7 | 1,666.9 |
| Total digestible nutrients (pounds) | 2,892.9 | 3,157.0 | 3,814.0 | 3,288.0 |
| Total digestible nutrients to 1 pound of butterfat (pounds) | 10.3 | 10.8 | 13.0 | 11.4 |
| Total digestible nutrients to 100 pounds of milk (pounds) | 37.2 | 41.1 | 49.7 | 42.6 |

Ratio of grain consumed to milk produced, 1:4.6.

TABLE 7. RECORDS FOR COWS PRODUCING ABOVE 9000 POUNDS OF MILK A YEAR

| | Wethersfield | Otsego | Perry Pike | Average |
|---|---|---|---|---|
| Number of cows, 32, or 3.8 per cent | 8 | 11 | 13 | ..... |
| Milk produced (pounds) | 10,128.7 | 9,787.9 | 9,983.6 | 9,966.7 |
| Butterfat produced (pounds) | 388.6 | 304.1 | 344.4 | 345.7 |
| Succulent roughage consumed (pounds) | 6,345.7 | 6,888.3 | 9,021.3 | 7,418.4 |
| Dry roughage consumed (pounds) | 3,020.2 | 1,935.2 | 2,871.2 | 2,608.9 |
| Grain consumed (pounds) | 2,375.1 | 2,351.0 | 2,132.0 | 2,286.0 |
| Total digestible nutrients (pounds) | 3,933.5 | 3,554.5 | 4,477.5 | 3,988.5 |
| Total digestible nutrients to 1 pound of butterfat (pounds) | 10.1 | 11.7 | 13.0 | 11.5 |
| Total digestible nutrients to 100 pounds of milk (pounds) | 38.8 | 36.3 | 44.8 | 40.0 |

Ratio of grain consumed to milk produced, 1:4.3.

### *Dry roughage uniform*

One of the first things noted is the uniformity in the average amount of dry roughage consumed per cow. Probably the groups as made up would include cows with nearly the same general capacity for roughage. A further reason for the uniformity in the amount consumed is the general and wise practice among dairymen of feeding to the cows, regardless of other factors, about all the roughage they will consume. Uniformity in this respect is about what would be expected. The dry roughage consumed ranged from 2261.9 to 2608.9 pounds a year.

### *Grain and succulent roughage varying*

As between the different groups, there is an increase in the succulent roughage and grain consumed which is fairly proportional to the increased

yield in each case of milk and butterfat. The question naturally rises, whether the increased production was in response to increased feeding of grain and succulent food or was due to the fact that the cows were better. Not all factors could be studied. There is no record as to individual breeding, evidences of capacity, weight, or similar factors. It must be assumed from the evidence obtained that the cows were fed largely according to their prospective capacity to use food to advantage. The testing association was depended upon to check the owners' judgment in this respect.

It is not possible to draw from the tables any definite measure of the value of either the succulent roughage or the grain. The fact is shown that large production followed proportionately the increased consumption per cow of succulent roughage and grain. It is hard to dissociate this fact from the combined influence of better cows and better management.

### *Nutrients for unit of product*

The test of efficiency is the total digestible nutrients required for the production of one hundred pounds of milk or one pound of butterfat. The last two items in tables 4, 5, 6, and 7 indicate by groups the average nutritive requirement for milk and fat production. The consistency with which the food requirement for production decreases as the yield increases is striking. Cows producing 5983 pounds of milk per annum (table 5) require 19.5 per cent less nutrients to produce 100 pounds of milk than do those averaging below 5000 pounds per annum (table 4). The former group (table 5), however, requires 10.6 per cent more nutrients per 100 pounds of milk than does the next higher group (table 6), where the average is 7708 pounds of milk per annum.

In the lowest-producing group (table 4), 58.5 pounds of nutrients was required for 100 pounds of milk and 13.4 pounds of nutrients for 1 pound of butterfat. In the third group (table 6), 42.6 pounds of nutrients was required for 100 pounds of milk and 11.4 pounds of nutrients for 1 pound of butterfat. Milk production was 37.3 per cent, and butterfat production 17.5 per cent, more expensive on the nutrient basis in the first group than in the third.

### *Ratio of grain consumed to milk produced uniform*

The cows in the different groups received about the same proportion of grain to milk produced. The ratio is more uniform than might at first have been expected. It ranges from 1:4.1 in table 4 to 1:4.6 in table 6. The cows producing from 7001 to 9000 pounds of milk (table 6) received the smallest proportion of grain to milk produced, while the poorest group of cows (table 4) received the largest proportion. In the

group producing above 9000 pounds, the grain consumption per cow was the largest for any group but the ratio of grain to milk was nearly the same as for cows in the 5000–7000-pound group.

The tendency in practice for inferior cows by groups to receive as much grain as the better cows indicates two things: (1) that the dairyman lacks appreciation of the relative efficiency of good and poor cows in the use of feed; and (2) that daily feeding practices are not closely correlated with the individual production secured.

This uniformity in the amount of grain fed suggests that some cows in the poorer groups were probably underfed, and also that there is constant danger of feeding the poor cows too much.

### THE TWO-YEAR-OLD COWS

Of the records taken, 11 per cent were from cows listed as two years of age. In some herds it was difficult to ascertain the exact ages, so that, of the 847 cows reported, doubtless not more than 11 per cent were two years old. The group report of such cows is given in table 8. This tabulation indicates that the two-year-old cows were nearly as good producers as average cows. They were better producers, and were certainly more efficient in the use of food, than the cows in the lowest group (table 4), to which some of them doubtless belonged. Therefore their influence distributed thru the groups has not tended to reduce the averages.

TABLE 8. RECORDS FOR COWS REPORTED AS TWO YEARS OLD

| | Wethersfield | Otsego | Perry Pike | Average |
|---|---|---|---|---|
| Number of cows, 93, or 11 per cent | 46 | 22 | 25 | ..... |
| Milk produced (pounds) | 4,209 | 4,626 | 4,377 | 4,404 |
| Butterfat produced (pounds) | 168 | 190 | 177 | 178 |
| Succulent roughage consumed (pounds) | 4,435 | 4,248 | 4,283 | 4,322 |
| Dry roughage consumed (pounds) | 2,537 | 1,885 | 1,845 | 2,089 |
| Grain consumed (pounds) | 898 | 1,345 | 783 | 1,009 |
| Total digestible nutrients (pounds) | 2,501 | 2,457 | 2,298 | 2,419 |
| Total digestible nutrients to 1 pound of butterfat (pounds) | 14.9 | 12.9 | 13.0 | 13.6 |
| Total digestible nutrients to 100 pounds of milk (pounds) | 59.4 | 53.1 | 52.5 | 54.9 |

### RELATIVE EFFICIENCY OF INDIVIDUALS

The foregoing discussion concerning the figures in tables 4 to 7 shows that in general, on the food basis, large-producing cows are the most economical per unit of product. This accords with careful trials and to a degree with general popular understanding. Such a calculation does

not, however, throw much light on the economic behavior of the individual. The necessity for individual performance records as a guide to economical production and effective herd improvement is inevitable. For these reasons the cow-testing associations and similar agencies must be kept continuously employed.

While the grouping in tables 4 to 7 shows that cows are fed roughly according to production, individual studies indicate that cows may not respond in production according to feeding. This is one of the most vital factors entering the business of milk production, and, whether it is an attribute of breeding or one of management, it calls for prompt attention.

The individual feed and production records of four cows, selected at random from the 847 records embodied in this report, are shown in table 9. The cows were all large consumers. Cows 1 and 2 were fed generously, received about the same quantity of digestible nutrients, and responded with a degree of efficiency proportionate to their production. The higher percentage of butterfat in the milk of cow 2 gives her a lower food cost per pound to produce it. She is a more economical producer of butterfat than cow 1, but is not so economical in the production of milk. These two cows represent satisfactory production at reasonable food cost.

TABLE 9. COMPARATIVE ECONOMY OF FOUR COWS

| | Cow 1 | Cow 2 | Cow 3 | Cow 4 |
|---|---|---|---|---|
| Nutrients consumed (pounds) | 4,205 | 4,015 | 6,273 | 5,367 |
| Milk produced (pounds) | 9,017 | 6,647 | 5,224 | 3,241 |
| Butterfat produced (pounds) | 379 | 409 | 212 | 110 |
| Nutrients required for 100 pounds of milk (pounds) | 46.6 | 60.4 | 120.1 | 165.6 |
| Nutrients required for 1 pound of butterfat (pounds) | 11.1 | 9.8 | 29.6 | 48.8 |

The records of cows 3 and 4 can profitably be compared with those of cows 1 and 2. While the production and the nutrients consumed by cows 3 and 4 are not exactly comparable, their relative efficiency suffers greatly in comparison with cows 1 and 2. Cow 3 required nearly three times as many pounds of nutrients for 100 pounds of milk as did cow 1, and three times as many pounds of nutrients for 1 pound of butterfat as did cow 2. Comparing cow 4 with cows 1 and 2 in the same manner, the difference is nearly in the ratio of 1:4 for the nutrients required for milk production and 1:5 for fat production. Cows 3 and 4 were large consumers but not economical producers.

These four cows had rations which were very similar in variety and nutritive value, and the proportions of grain, silage, and hay were fairly uniform. The length of period on pasture favored cows 3 and 4; cows 1 and 2 had the shortest pasture period.

## ACCURACY OF THE RESULTS

After the feeding and production records of the 847 cows in the cow-testing associations considered in this bulletin were tabulated, it seemed desirable to determine how such data would compare with similar calculations from herd records kept with greater individual accuracy. While strict conformity could hardly be expected, a reasonable coincidence of results would enhance the value of the test-association data.

In Bulletin 167 of the Wisconsin Agricultural Experiment Station, the feed and production records of 27 cows for one year are reported in such form as to be easily compared with the data at hand. This report includes a herd in which there is a fair range as to breeding and quality of cows. While this herd was limited in numbers, perhaps, and above the average in production, it must be recognized that complete data could hardly be found in a herd of a different sort.

The feed records of the cows in this herd were tabulated as to the kind and quantity of food consumed, and the nutrients were calculated. The cows were then grouped according to production exactly as for the data given in tables 4 to 7. A brief comparison of the results is presented in table 10:

TABLE 10. COMPARISON OF TEST-ASSOCIATION RESULTS WITH DATA FROM A HERD FOR WHICH ACCURATE FEED RECORDS WERE AVAILABLE

| | Production below 5000 pounds | | Production from 5000 to 7000 pounds | | Production from 7001 to 9000 pounds | | Production above 9000 pounds | |
|---|---|---|---|---|---|---|---|---|
| | Wisconsin | New York | Wisconsin | New York | Wisconsin | New York | Wisconsin | New York |
| Milk produced (pounds) | 3,907.0 | 3,925.6 | 5,852.9 | 5,982.8 | 7,877.7 | 7,708.4 | 10,688.0 | 9,966.7 |
| Butterfat produced (pounds) | 188.4 | 171.9 | 295.6 | 246.0 | 336.0 | 287.9 | 364.0 | 345.7 |
| Succulent roughage consumed (pounds) | 6,684.0 | 3,866.9 | 6,499.0 | 4,701.3 | 7,186.0 | 5,869.3 | 8,318.0 | 7,418.4 |
| Dry roughage consumed (pounds) | 1,009.0 | 2,365.5 | 996.0 | 2,261.9 | 1,040.0 | 2,265.6 | 1,217.0 | 2,608.9 |
| Grain consumed (pounds) | 1,049.5 | 946.3 | 1,521.3 | 1,370.2 | 1,699.0 | 1,666.9 | 2,043.0 | 2,286.0 |
| Total digestible nutrients (pounds) | 2,479.7 | 2,296.8 | 2,808.5 | 2,821.1 | 3,093.5 | 3,288.0 | 3,649.5 | 3,988.5 |

There is substantial correspondence between the two groups in the amount of milk and butterfat produced. The Wisconsin cows received about 31 per cent more succulent roughage, averaging the groups together,

than did the New York cows. The latter, however, were fed about 123 per cent more dry roughage than were the former. To offset the smaller quantity of hay or dry forage received, the Wisconsin cows, in all except the highest-producing group, got more grain than did the New York cows. Making the comparison on the amount of total digestible nutrients fed, it is seen that there is substantial correspondence between the amounts of nutrients in the two cases supplied to cows of similar production. In other words, the testing-association calculations check remarkably well with similar data from a herd for whose records careful individual weights were taken. The Wisconsin feed records do not include pasture, which was limited in amount. This renders the two sets of data still more comparable.

## DISTRIBUTION OF COSTS

The cost of producing milk is derived from many sources. Some elements are more important and larger than others. The total cost of production is likely to vary from farm to farm. It is therefore very difficult to determine at any time or for any given place the exact cost of milk production. It is highly desirable, however, that the general public, as well as the producer, shall have a fuller knowledge and appreciation of the subject, for it is no longer a private or individual problem but has become a leading public question. It demands more intelligent study than the public has thus far given to it.

It has not been the purpose of this bulletin to go further than to report certain facts obtained with reference to the quantity and the nutritive value of feeds as they relate to commercial milk production practices in New York State. The relation of wise feeding and good cows to profits will always be an intimate one. Feed, labor, and quality of the cow are susceptible of a wide range of control by the dairyman. Many of the other factors entering into the cost of milk are rather definitely fixed.

The most pressing question for the milk producer is that of feed supplies. The feed cost of milk production may represent from 50 to 60 per cent of the total cost. The foregoing tables indicate the kinds and quantities of feed required under the conditions indicated, and afford a fair basis for estimating the cost. If to the feed the cost of labor is added, an item representing at least 70 per cent of the cost of production is obtained. Feed and labor each have natural limits beyond which they cannot go in production. These elements overshadow the problem so completely, however, that to deny the possibility of dealing with them more effectively is to ignore the facts.

SUMMARY

This bulletin reports the yearly production and feed records (except pasture) of 847 cows which were included in cow-testing associations in New York. The cows were studied in groups as follows:

335 cows, or 39.6 per cent, producing less than 5000 pounds of milk;
368 cows, or 43.4 per cent, producing from 5000 to 7000 pounds of milk;
112 cows, or 13.2 per cent, producing from 7001 to 9000 pounds of milk;
32 cows, or 3.8 per cent, producing above 9000 pounds of milk;
93 cows, or 11 per cent, listed as two-year-olds with an average production of 4404 pounds of milk.

The average consumption of dry roughage was practically uniform in the different groups.

The larger-producing groups received proportionately increased amounts of silage and grain.

This increased consumption of nutrients per group was consistently related to a decrease in nutrients required for a unit of product.

The ratio of grain fed to milk produced was practically uniform in all groups. This indicates a tendency in feeding practice to apportion grain to cows without due regard to their individual merit.

Individuals may vary greatly in the efficiency with which they use nutrients. This variation may have as great a ratio as $1:3\frac{1}{2}$ in the nutrients required by individuals for the production of 100 pounds of milk.

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AGRICULTURAL EXPERIMENT STATION

# EXPERIMENTS IN FERTILIZING A CROP ROTATION

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# EXPERIMENTS IN FERTILIZING A CROP ROTATION

T. L. Lyon

Some years ago experiments in fertilizing timothy hay in a rotation of corn, oats, wheat, and hay were conducted by this experiment station.[1] The timothy remained on the land for three years of the six occupied by the rotation and was fertilized each year, but the grain crops that followed received no fertilizer. A very striking result of these tests was the marked benefit derived from the fertilizers, not only thru the increased yields of hay but also by the after effects on the corn crop. The benefit to the corn appears to have been due in large degree to the better sod resulting from the fertilizer treatment, which furnished a larger quantity of organic matter to be plowed under on the fertilized land.

The great advantage derived from the use of fertilizer on timothy in the tests referred to raised the question whether the results would have been equally marked if the fertilizer had been applied to the grain crops instead of to the grass. For the purpose of comparing these practices a new set of experiments was undertaken, the results of which it is the purpose of this bulletin to describe.

## SOIL ON WHICH THE EXPERIMENTS WERE CONDUCTED

That the fertilizers proved so beneficial when applied to timothy hay in the previous experiments was no doubt due in part to the fact that the soil used was a most excellent one for timothy production. The experiments here reported were conducted on soil of similar type but in a much better state of fertility. It is a heavy clay loam containing a rather good supply of plant-food material, very retentive of moisture, slow to dry in the spring, and likely to puddle if worked when wet. As it warms slowly in the spring its nitrogen becomes available very slowly, and it is probably for this reason that nitrate of soda greatly helps the early growth of the grass and may be used profitably in quantities as large as 300 pounds to the acre. In considering the results of the experiments to be described, it must be remembered that the soil used was better adapted to hay production than to any of the cereals used with the possible exception of wheat. Another condition somewhat more favorable to the practice of fertilizing the hay crops was the fact that the experiment began with the hay crops, and consequently where they were fertilized

[1] Experiments concerning the top-dressing of timothy and alfalfa. By T. Lyttleton Lyon and James A. Bizzell. Cornell Univ. Agr. Exp. Sta. Bul. 339:117–144. 1913.

the grain following them had the benefit of the residual effect. While this was not true of the plats fertilized for grain, it was offset in part by the high state of fertility of the soil.

Corn grows poorly on this soil unless a large quantity of organic matter has recently been added, which accounts for the good effects of thicker sod produced by fertilizer. Even for oats this soil is rather too heavy.

The soil was in very good condition at the time the experiments were started. There had recently been a crop of peas plowed under, which supplied a considerable quantity of nitrogen and organic matter. The large yields of corn were probably due to this organic matter. Lime was applied to all the plats at the rate of four tons of marl to the acre.

The conditions of the test were somewhat in favor of the practice of fertilizing for the hay rather than for the grain crops. If, on the other hand, the soil had been one well adapted to the production of corn, the results might have been different. In interpreting the results it will be well to keep in mind that they are probably not of universal application, but that they may be a guide to good fertilizer practice on soils resembling the one used in this experiment, which is perhaps typical of the good timothy-producing land of the State. For this reason the experiment may be of interest to those farmers who have made a practice of devoting three years or more of each rotation to hay because their land was well suited to its culture.

### APPLICATION OF FERTILIZERS

Since the rotation comprised three years of grass and three years of grain, it was possible to give the fertilizer treatment thru the same period of time to the two kinds of crops, but on different plats. It did not seem advisable, however, to give exactly the same treatment of commercial fertilizer to the grass and the grain crops, since the fertilizer formula generally regarded as best for grass differs from that usually accorded to the cereals, especially corn. Except on those plats on which farm manure was used, the fertilizer treatment for grass differed from that used for the grain crops. The comparison of the practice of fertilizing for grass or for grain may be separated into three tests, the results of which are set forth, respectively, in tables 1, 2, and 3 (pages 23, 24, and 26).

In 1912 manure was spread on April 23-24; nitrate of soda and muriate of potash were applied on April 25, and the acid phosphate and floats on May 1; hay was cut on June 29; there was a good stand of red clover with the timothy. In 1913 manure was spread on April 2 and the commercial fertilizers on April 8; hay was cut on July 14. In 1914 manure was spread on April 17 and the other fertilizer on April 16-17. For the corn raised in 1915, manure was applied on April 23 and the commercial

fertilizer on May 17; corn was planted on May 18 and cut on October 6-7. In 1916 fertilizer was applied for oats on May 3; the oats were planted on the same date and were cut on August 10. Fertilizer was applied for wheat on September 14 and the wheat was drilled on the same date.

### METHOD OF COMPUTING FINANCIAL RESULTS

In order to make a comparison of the monetary returns from the different fertilizer treatments, each crop was given a certain value per bushel or ton based on average prices that obtained for several years preceding the war, these prices being the same as were used in computing financial results from the experiments previously mentioned. The price allowed for hay was $12 a ton, for corn 66 cents a bushel and $3 a ton for stover, for wheat 90 cents a bushel, for oats 43 cents a bushel, and for both wheat and oat straw $5 a ton. In a similar way values were given to the fertilizers used, based on average prices that ruled during several years prior to 1914. Nitrate of soda was considered as costing $56 a ton when spread on the field, muriate of potash $46, acid phosphate $16 (a 16-per-cent grade was used), and farm manure $1.50.

Owing to the fact that the prices of farm products had undergone very great changes between 1914 and 1918 and the percentage increase in price had been greater for cereals than for hay, it was evident that the financial results of any system of fertilization for this rotation would be different under present prices. It even seemed possible that any advantage which might have been gained from fertilizing grass before the war would be lost at the present high prices for grain. Therefore computations of the values of the crops produced were made on the basis of present prices as well as those given above. For current prices the approximate figures reported for New York State on July 1, 1918, by the Federal Department of Agriculture and the Farm Bureaus of New York State, were adopted. These were as follows: hay $16.40 a ton, corn $1.925 a bushel, oats 96 cents a bushel, wheat $2.10 a bushel. Stover and straw were assumed to have undergone the same relative increase as hay, which would bring them to $4 and $6.50 a ton, respectively.

In all three of the experiments the total values of all crops in the rotation were greater when the fertilizers were applied to the grass than when they were applied to the grain crops. With prices for the products considered on the July 1, 1918, basis, the advantage is still with the practice of fertilizing for hay.

Calculations of the financial results of the experiments at present prices were not extended to the fertilizer prices, because of the abnormal condition of such prices at the present time. Some idea may be obtained as to the advisability of fertilizing for hay or for grain, from the relative

values of all the crops produced in the rotation in which fertilizers were used on the grass as compared with those in the rotation fertilized for grain.

### COMPARISON OF THE PRACTICE OF FERTILIZING THE HAY CROPS WITH THAT OF FERTILIZING THE GRAIN CROPS

The first of the tests involves the use of moderate quantities of commercial fertilizer applied to each of the grain crops as compared with somewhat similar quantities applied to each of the grass crops. Inasmuch as the fertilizer formula for grass calls for more nitrogen than does that for grain, the quantity of nitrate of soda applied to the grass was greater. Furthermore, the total quantity of fertilizer applied to the grass was greater, because it was desired to limit the cost of the fertilizer on grain to a point that might be expected to yield a profit. The quantity of fertilizer applied to each crop, and the yields and value, together with the cost of the fertilizer and the value of the increased crops over the cost of the fertilizer, are stated in table 1. It will be noted that the total quantities of acid phosphate and muriate of potash for the rotation were the same whether applied to grass or to grain, but that the quantity of nitrate of soda was less for the grain plats.

It is shown in table 1 that the use of the fertilizer on the grass was much more effective than its use on the grain crops. The hay yields were increased by a little more than a half ton to the acre each year thru the use of the fertilizer. On the other hand, the application of fertilizer to the grain crops did not have much effect except on the wheat, which was increased by a little more than two bushels to the acre. It must be remarked that the yields of grain are large, the corn producing 61 bushels, the oats 35 bushels, and the wheat 34 bushels, to an acre on the unfertilized plats. When grain yields are as large as they were on this land, fertilizers are likely to have less relative effect than if the soil were in poorer condition. It is also worthy of remark that while the yield of hay on the unfertilized plats amounted to $2\frac{3}{4}$ tons to the acre, the fertilizer applications raised the average yield to nearly $3\frac{1}{3}$ tons. It is evident that the hay responded more generously to fertilizer treatment than did any of the grain crops.

The financial statement also shows the advantage to be derived from applying the fertilizers to the grass rather than to the grain, for, while the accounts for the entire rotation show a monetary loss from those plats on which the fertilizer was applied to the grain, they exhibit a gain of more than $9 an acre from the plats on which the fertilizer was applied to the grass. Even at prices ruling on July 1, 1918, the value of the crops produced on the plats fertilized for grass as compared with those fertilized for grain was greater than when based on pre-war prices. This is to be explained by the fact that the increased yields of grass were followed by increased grain crops.

TABLE 1. RESULTS OF APPLYING FERTILIZER TO GRASS AS COMPARED WITH APPLYING IT TO GRAIN, IN A ROTATION OF CROPS

| Year | Crop raised | Fertilizer application per acre | |
|---|---|---|---|
| | | Plats fertilized for grain | Plats fertilized for hay |
| 1912 | Timothy and clover | No fertilizer | Nitrate of soda, 92 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1913 | Timothy | No fertilizer | Nitrate of soda, 68 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1914 | Timothy | No fertilizer | Nitrate of soda, 128 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1915 | Corn | Acid phosphate, 184 lbs.<br>Muriate of potash, 56 lbs. | No fertilizer |
| 1916 | Oats | Nitrate of soda, 36 lbs.<br>Acid phosphate, 100 lbs.<br>Muriate of potash, 56 lbs. | No fertilizer |
| 1917 | Wheat | Nitrate of soda, 96 lbs.<br>Acid phosphate, 100 lbs.<br>Muriate of potash, 56 lbs. | No fertilizer |
| Crop yields per acre | | | |
| | Hay (yearly average for three years) | 2.77 tons (5,550 lbs.) | 3.32 tons (6,637 lbs.) |
| | Corn | Grain 61.0 bu. (4,270 lbs.)<br>Stover 2.16 tons (4,320 lbs.) | Grain 60.6 bu. (4,240 lbs.)<br>Stover 2.30 tons (4,610 lbs.) |
| | Oats | Grain 40.3 bu. (1,290 lbs.)<br>Straw 1.07 tons (2,145 lbs.) | Grain 40.0 bu. (1,280 lbs.)<br>Straw 1.06 tons (2,122 lbs.) |
| | Wheat | Grain 39.2 bu. (2,350 lbs.)<br>Straw 1.80 tons (3,610 lbs.) | Grain 36.8 bu. (2,165 lbs.)<br>Straw 1.62 tons (3,240 lbs.) |
| Total value of crops per acre based on pre-war prices | | | |
| | Fertilized as above | $211.21 | $227.05 |
| | Not fertilized | 202.90 | 202.90 |
| | Increased value due to fertilizer | $8.31 | $24.15 |
| | Cost of fertilizer | 9.81 | 14.99 |
| | Gain* or loss from use of fertilizer | −$1.50 | $9.16 |
| | Increased value of crops per dollar invested in fertilizer | $0.85 | $1.61 |
| | Total value of crops per acre based on prices of July 1, 1918 | $402.24 | $419.69 |
| Difference in favor of fertilizing grass | | | |
| | Based on pre-war prices | $15.84 | |
| | Based on prices of July 1, 1918 | 17.45 | |

*Gain in this and following tables means the value of the increased crops over the cost of the fertilizer.

## COMPARISON OF THE PRACTICE OF MANURING THE HAY CROPS WITH THAT OF MANURING A GRAIN CROP

In the second experiment five tons of farm manure was applied to each of the three hay crops, and to offset this fifteen tons of similar

TABLE 2. RESULTS OF APPLYING FARM MANURE TO GRASS AS COMPARED WITH APPLYING IT TO GRAIN, IN A ROTATION OF CROPS

| Year | Crop raised | Fertilizer application per acre | |
|---|---|---|---|
| | | Plats manured for grain | Plats manured for hay |
| 1912 | Timothy and clover | No fertilizer | Farm manure, 5 tons |
| 1913 | Timothy | No fertilizer | Farm manure, 5 tons |
| 1914 | Timothy | No fertilizer | Farm manure, 5 tons |
| 1915 | Corn | Farm manure, 15 tons | No fertilizer |
| 1916 | Oats | No fertilizer | No fertilizer |
| 1917 | Wheat | Nitrate of soda, 24 lbs.<br>Acid phosphate, 100 lbs.<br>Muriate of potash, 16 lbs. | Nitrate of soda, 24 lbs.<br>Acid phosphate, 100 lbs.<br>Muriate of potash, 16 lbs. |
| Crop yields per acre | | | |
| Hay (yearly average for three years) | | 2.77 tons (5,550 lbs.) | 3.14 tons (6,280 lbs.) |
| Corn | | Grain 73.9 bu. (5,170 lbs.)<br>Stover 3.07 tons (6,140 lbs.) | Grain 68.6 bu. (4,800 lbs.)<br>Stover 2.45 tons (4,910 lbs.) |
| Oats | | Grain 40.6 bu. (1,300 lbs.)<br>Straw 1.11 tons (2,222 lbs.) | Grain 34.7 bu. (1,110 lbs.)<br>Straw 1.04 tons (2,080 lbs.) |
| Wheat | | Grain 38.6 bu. (2,315 lbs.)<br>Straw 1.80 tons (3,595 lbs.) | Grain 40.1 bu. (2,472 lbs.)<br>Straw 1.76 tons (3,530 lbs.) |
| Total value of crops per acre based on pre-war prices | | | |
| Fertilized as above | | $221.80 | $229.13 |
| Not fertilized | | 202.90 | 202.90 |
| Increased value due to fertilizer | | $18.90 | $26.23 |
| Cost of fertilizer | | 24.34 | 24.34 |
| Gain or loss from use of fertilizer | | −$5.44 | $1.89 |
| Increased value of crops per dollar invested in fertilizer | | $0.78 | $1.08 |
| Total value of crops per acre based on prices of July 1, 1918 | | $429.90 | $434.36 |
| Difference in favor of manuring grass | | | |
| Based on pre-war prices | | $7.33 | |
| Based on prices of July 1, 1918 | | $4.46 | |

manure was plowed under for the corn crop on another set of plats which had received no manure on the hay crops. The total quantity of manure used in each set of plats was fifteen tons. A small quantity of fertilizer was applied to the wheat on both sets of plats. The treatments and results are shown in table 2.

These tabulated results show that the annual dressing of five tons of farm manure produced an average annual increase in yield of less than a half ton of timothy hay to the acre. To offset this the application of fifteen tons of farm manure increased the corn crop by something more than five bushels to the acre, and the residual effect on the oats crop produced an increase of six bushels.

On the land on which manure was used for top-dressing timothy the financial gain was slight, while the application for corn resulted in a loss; but had the manure been valued at $1 a ton there would have been a profit from the use of manure in both rotations. When considered with reference to the best use of small quantities of farm manure in a rotation of this kind on the soil in question, the results indicate that this fertilizer is most profitably used on the hay crops.

Another experiment was conducted with this end in view, which differed from the experiment just described in that the grass received an annual application of ten tons of farm manure on one piece of land, while on the other the farm manure was plowed under for corn at the rate of thirty tons to the acre, none being applied to the grass. The results of this test are shown in table 3.

It is seen by table 3 that this test confirms the previous one indicating that farm manure is better applied to the grass than to the corn under the conditions of the experiments. It will also be noticed that in this case the application of ten tons of manure to the grass each year for three years gave about the same financial gain that was derived from the use of five tons annually. On the other hand, thirty tons applied for corn increased the loss over the application of fifteen tons for the same crop. Farm manure may therefore be used with profit in larger quantities for grass than for corn on this soil. When prices for crops are as low as those used in making these calculations, farm manure must be delivered on the field at a lower value than $1.50 a ton if it is to be profitable on a soil already in a good state of fertility.

### COMPARISON OF THE PRACTICE OF WITHHOLDING POTASH FROM THE FERTILIZER MIXTURE WITH THAT OF USING A MODERATE QUANTITY

The following experiment was begun several years before the war had caused a shortage in the supply of potash. It was undertaken because the soil on which the experiment was conducted contains a large quantity of potash, amounting to 64,000 pounds to an acre foot of surface soil,

and since a moderate application — as, for instance, 56 pounds of muriate of potash — would add only 28 or 29 pounds more to the acre, there seemed to be a reasonable doubt whether a potash fertilizer could be profitably used. Applications of moderate quantities of nitrate of soda and acid phosphate were given each year for three years to one set of timothy plats, and the same quantity of nitrate of soda and acid phos-

TABLE 3. RESULTS OF APPLYING A LARGER QUANTITY OF FARM MANURE TO GRASS AS COMPARED WITH APPLYING IT TO GRAIN, IN A ROTATION OF CROPS

| Year | Crop raised | Fertilizer application per acre | |
|---|---|---|---|
| | | Plats manured for grain | Plats manured for hay |
| 1912.. | Timothy and clover | No fertilizer..... | Farm manure, 10 tons |
| 1913.. | Timothy.... | No fertilizer..... | Farm manure, 10 tons |
| 1914.. | Timothy.... | No fertilizer..... | Farm manure, 10 tons |
| 1915.. | Corn..... | Farm manure, 30 tons..... | No fertilizer |
| 1916.. | Oats..... | No fertilizer..... | No fertilizer |
| 1917.. | Wheat..... | Nitrate of soda, 24 lbs.....<br>Acid phosphate, 100 lbs.....<br>Muriate of potash, 16 lbs.... | Nitrate of soda, 24 lbs.<br>Acid phosphate, 100 lbs.<br>Muriate of potash, 16 lbs. |
| Crop yields per acre | | | |
| Hay (yearly average for three years).. | | 2.77 tons (5,550 lbs.) | 3.52 tons (7,077 lbs.) |
| Corn..... | | Grain 80.1 bu. (5,610 lbs.)<br>Stover 4.11 tons (8,230 lbs.) | Grain 72.6 bu. (5,080 lbs.)<br>Stover 2.96 tons (5,930 lbs.) |
| Oats..... | | Grain 41.9 bu. (1,340 lbs.)<br>Straw 1.17 tons (2,337 lbs.) | Grain 37.2 bu. (1,194 lbs.)<br>Straw 1.14 tons (2,282 lbs.) |
| Wheat..... | | Grain 44.9 bu. (2,692 lbs.)<br>Straw 2.18 tons (4,355 lbs.) | Grain 42.4 bu. (2,545 lbs.)<br>Straw 1.91 tons (3,815 lbs.) |
| Total value of crops per acre based on pre-war prices | | | |
| Fertilized as above. | | $237.26 | $250.94 |
| Not fertilized..... | | 202.90 | 202.90 |
| Increased value due to fertilizer..... | | $34.36 | $48.04 |
| Cost of fertilizer... | | 46.84 | 46.84 |
| Gain or loss from use of fertilizer... | | —$12.48 | $1.20 |
| Increased value of crops per dollar invested in fertilizer | | $0.73 | $1.03 |
| Total value of crops per acre based on prices of July 1, 1918..... | | $462.52 | $470.36 |
| Difference in favor of manuring grass | | | |
| Based on pre-war prices..... | | $13.68 | |
| Based on prices of July 1, 1918..... | | $7.84 | |

phate, together with a moderate quantity of muriate of potash, was applied at the same time to another set of timothy plats. The returns for the entire rotation are given in table 4:

TABLE 4. RESULTS OF APPLYING MODERATE QUANTITIES OF COMPLETE FERTILIZER TO GRASS CROPS AS COMPARED WITH APPLICATION OF NITROGEN AND PHOSPHORUS ONLY

| Year | Crop raised | Fertilizer application per acre | |
|---|---|---|---|
| | | No potash in fertilizer | Potash in fertilizer |
| 1912 | Timothy and clover | Nitrate of soda, 92 lbs.<br>Acid phosphate, 128 lbs. | Nitrate of soda, 92 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1913 | Timothy | Nitrate of soda, 68 lbs.<br>Acid phosphate, 128 lbs. | Nitrate of soda, 68 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1914 | Timothy | Nitrate of soda, 128 lbs.<br>Acid phosphate, 128 lbs. | Nitrate of soda, 128 lbs.<br>Acid phosphate, 128 lbs.<br>Muriate of potash, 56 lbs. |
| 1915 | Corn | No fertilizer | No fertilizer |
| 1916 | Oats | No fertilizer | No fertilizer |
| 1917 | Wheat | No fertilizer | No fertilizer |
| Crop yields per acre | | | |
| Hay (yearly average for three years) | | 3.23 tons (6,470 lbs.) | 3.32 tons (6,636 lbs.) |
| Corn | | Grain 60.0 bu. (4,200 lbs.)<br>Stover 1.90 tons (3,800 lbs.) | Grain 60.6 bu. (4,240 lbs.)<br>Stover 2.30 tons (4,610 lbs.) |
| Oats | | Grain 33.4 bu. (1,070 lbs.)<br>Straw 0.93 ton (1,870 lbs.) | Grain 40.0 bu. (1,280 lbs.)<br>Straw 1.06 tons (2,122 lbs.) |
| Wheat | | Grain 37.5 bu. (2,250 lbs.)<br>Straw 1.60 tons (3,202 lbs.) | Grain 36.1 bu. (2,165 lbs.)<br>Straw 1.62 tons (3,240 lbs.) |
| Total value of crops per acre based on pre-war prices | | | |
| Fertilized as above | | $220.29 | $227.03 |
| Not fertilized | | 202.90 | 202.90 |
| Increased value due to fertilizer | | $17.39 | $24.13 |
| Cost of fertilizer | | 11.12 | 14.99 |
| Gain from use of fertilizer | | $6.27 | $9.14 |
| Increased value of crops per dollar invested in fertilizer | | $1.56 | $1.61 |
| Total value of crops per acre based on prices of July 1, 1918 | | $409.60 | $419.69 |
| Difference in favor of potash fertilizer | | | |
| Based on pre-war prices | | $6.74 | |
| Based on prices of July 1, 1918 | | $10.09 | |

The effect of the potash fertilizer was to increase the yield of hay and possibly to slightly increase some of the grain crops — the latter may have been an indirect effect. The cost of the potash fertilizer was less than the increased value of the crops, and under the conditions of the experiment the use of this constituent would appear to be advisable. The native soil potash, altho large in amount, does not become available to plants rapidly enough to supply the needs of large crops of timothy.

## SUMMARY

The experiments here described were designed to test the practice of fertilizing the grass in a crop rotation with that of fertilizing the grain. The rotation consisted of three years in hay, followed by corn, oats, and wheat.

The soil used for the experiments was better suited to the production of hay than of grain, and was in a good state of fertility. It is representative of the good timothy soils of the State.

A moderate quantity of a complete commercial fertilizer applied during each of the three years the land was in timothy was more profitable than a somewhat similar fertilizer applied to corn, oats, and wheat.

The application of five tons per acre of farm manure to each of three timothy crops proved to be more effective than fifteen tons applied to the corn alone in the rotation.

When farm manure was applied at the rate of ten tons per acre to the grass and thirty tons to the corn, the yields of crops were increased but not proportionately to the cost of the manure. Under the conditions of the experiment the application of fifteen tons per acre of manure during the rotation proved to be better management than the use of thirty tons.

In a test of commercial fertilizer containing potash as well as nitrogen and phosphoric acid applied annually to the grass, as compared with the same quantities of the last two constituents only applied to the same crops, the use of potash at pre-war prices appeared to be profitable.

# APPENDIX

## TECHNICAL PROCEDURE

For the benefit of persons who may wish to know something of the methods used in conducting these experiments and in calculating the results, a brief explanation is here given.

### METHODS USED IN THE FIELD

The experiments were conducted on Caldwell Field, on plats of land 0.01 acre in area, measuring 43.6 by 10 feet with a space of two feet between the plats. The intervening spaces were always planted with the same crops as those on the plats, as were also the plat margins along the roadways. Before harvesting the crops from the plats the plants between the plats and along the margins were removed.

Every third plat was used as a check and received no fertilizer. Each fertilizer treatment to be tested was applied on four plats, distributed as uniformly as possible over the area occupied by the experiment.

### METHOD OF ESTIMATING EFFECT OF FERTILIZERS

The normal yield for each test plat was calculated from the two nearest check plats, on the assumption that the productivity of the land underwent a gradual change from one check plat to the next. The apparent increases or decreases for each set of four replicate test plats were averaged. The yield per acre for any treatment was, for convenience, assumed to be the average for all check plats plus or minus the average increase or decrease for the four replicate test plats in question. The value of the crop was based on this figure.

For example, in order to calculate the effect of the fertilizer treatment from the yields on plats 7407, 7426, 7617, and 7636 in 1914, as given in table 1, the procedure would be as follows: The actual yield of hay on plat 7407 was 81 pounds; the yields on plats 7405 and 7409 were 58 and 57 pounds, respectively. Assuming that there is a gradual change between plats 7405 and 7409, it would be considered that the normal yields for the intermediate plats, if the treatments had been similar to the checks, would be approximately as follows:

| | |
|---|---|
| Plat 7406 | 57.8 pounds |
| Plat 7407 | 57.5 pounds |
| Plat 7408 | 57.3 pounds |

As the actual yield on plat 7407 was 81 pounds, the apparent increase due to the treatment on this plat was the difference between the actual yield and the normal yield, or 23.5 pounds. In the same way the effect of the treatment is calculated for plats 7426, 7617, and 7636, and is found to be an increase of 6.5 pounds, 25 pounds, and 21 pounds, respectively. The average of these four values is taken as the apparent increase due to the treatment on the soil used in the experiment.

Such a calculation precludes a statement of the acre yield due to any treatment, and for the average reader it is desirable to express results in acre yields. Merely as a matter of convenience, therefore, the apparent increase as calculated above is added to the average of all checks used in the experiment, and the result is taken as the acre yield on which is based the value of the crop.

To ascertain whether the difference in yield was significant between any two sets of plats that received different treatments, the probable error for the increased yield of each set of four plats was calculated by means of the formula

$$\text{P. E.} = \pm 0.8453 \frac{\Sigma\ (+\ \text{d})}{\text{n}\sqrt{\text{n}-1}}$$

in which $\Sigma\ (+\ \text{d})$ denotes the sum of the deviations of every plat yield from the mean of the four, their signs being disregarded, and $n$ represents the number of plats, which was four in each case.

The probable error for each set of plats being calculated, the next step was to ascertain whether the yields of certain sets of plats could be compared, with the practical

certainty that the differences were due to the treatments accorded the plats. The probable error for the difference between any two sets of plats was calculated by means of the formula

$$E = \sqrt{E_1^2 + E_2^2}$$

in which $E_1$ is the probable error for one set of plats and $E_2$ the probable error for the set of plats with which the comparison is to be made. Assuming that the odds must be 30 to 1 to insure that the differences in yield are due to the treatments given the plats and not to normal variations, the probable error for the difference between the two sets of plats when multiplied by 3.8 must be less than the difference in yield. This test has been applied to the total yields of hay for the years 1912, 1913, and 1914, in each one of the tables presented in the manuscript.

It may be remarked that there were a number of other tests in the experiments which failed to show significant differences in yield and which were omitted from this report for that reason.

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